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Diatom responses to long-term climate and sea-level rise at a low-elevation lake in coastal British Columbia, Canada

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Abstract. Diatom assemblages from Lake Stowell, a low-elevation lake in coastal British Columbia, were used to assess limnological responses associated with changes in relative sea level (RSL) and climate over the past 14,500 yr. Marine diatom taxa dominated the early record and disappeared abruptly by 14,000 cal yr BP in response to glacio-isostatic uplift and an ensuing decrease in RSL. A brackish-freshwater phase from 14,200 to 13,400 cal yr BP was marked by increases in several diatom taxa with tolerance for low-to-moderate salinity, after which assemblages became strictly freshwater. Biostratigraphic changes in both diatom and chironomid assemblages from Lake Stowell occurred more or less simultaneously throughout the record in response to long-term changes in climate forcings, such as temperature. Increases in cold-adapted diatom (*Staurosirella pinnata*, *Staurosira construens*, *Staurosirella dubia*) and chironomid (*Sergentia*) taxa between 12,900 and 11,700 cal yr BP coincided with Younger Dryas cooling, suggesting a direct link with summer temperature. Shifts in aquatic biota also reflected indirect mechanisms through which climate affected the Lake Stowell ecosystem, for example, by altering thermal stratification, disturbance regimes, and nutrient concentrations. For instance, high summer insolation and warm summer temperatures from 11,700 to 8500 cal yr BP were associated with greater abundances of *Stephanodiscus hantzschii* and especially *Aulacoseira subarctica*. A concurrent opening of the forest canopy triggered by warming would have exposed the lake to strong winds and enhanced mixing, favoring these more heavily silicified taxa as an indirect consequence of climatic changes. Diatom assemblages appear to have been impacted by the deposition of Mount Mazama tephra at 7600 cal yr BP; a notable increase in *Aulacoseira tenella* suggests a response to increased silica availability in association with tephra deposition.

Key words: chironomids; diatoms; Holocene; isolation basin; lake sediments; Mazama tephra; paleolimnology; relative sea level.

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INTRODUCTION

In southern British Columbia, patterns of post-glacial climate have been inferred at local and regional scales from paleo-records of terrestrial pollen (Heusser et al. 1985, Pellatt et al. 2001, Walker and Pellatt 2003, Galloway et al. 2007) and aquatic biota (Palmer et al. 2002, Rosenberg et al. 2004, Lemmen and Lacourse 2018).

Paleoclimate reconstructions show that temperature oscillated over rather broadscales; for instance, a generally cooler late-glacial period culminated in warming during the Bølling/Ållerød interstadial (14,640–12,850 cal yr BP; Kuehn et al. 2014), followed by a short-term cooling during the Younger Dryas (12,900–11,700 cal yr BP; Kienast and McKay 2001, Lemmen and Lacourse 2018). A subsequent

warm, dry period occurred during the early to middle Holocene (11,700–7800 cal yr BP), leading into cooler temperatures and increased moisture availability toward the present (Brown et al. 2006, Voit et al. 2014). A solid understanding of baseline responses in terrestrial and aquatic ecosystems to these long-term shifts in climate is especially important within the context of future warming and anthropogenic impacts.

In addition to long-term changes in climate, sea-level histories of coastal areas in southern British Columbia have been studied closely (Hutchinson et al. 2004, James et al. 2009, Roe et al. 2013, Shugar et al. 2014, Fedje et al. 2018). These studies offer insights into patterns of basin isolation and lake development following deglaciation of the Cordilleran Ice Sheet, and subsequent isostatic uplift and decreases in relative sea level (RSL) after ~14,000 cal yr BP. Precise dating of the floristic changes in diatom (class: Bacillariophyceae) assemblages is typically used to constrain marine-to-freshwater transitions (Hutchinson et al. 2004, James et al. 2009, Fedje et al. 2018), as these aquatic bio-indicators have a broad range of salinity preferences among individual taxa (van Dam et al. 1994, Fedje et al. 2018). Diatoms are widely used in paleolimnological studies given that they are also sensitive to other environmental forcings, for example, air and water temperature, lake thermal stratification, nutrient fluxes, tephra deposition, and others (Smol et al. 2005, Rühland et al. 2015). In studies from southern British Columbia (Bennett et al. 2001, Galloway et al. 2007, Michelutti et al. 2016) and elsewhere (Rosen et al. 2001, Rosen et al. 2003, Neil and Gajewski 2017, 2018), multi-proxy approaches incorporating combinations of diatom data with chironomid, pollen, and/or geochemical data have been used to provide detailed and rich histories of environmental change, to assess links between biota from various trophic levels and their responses to external forcings, as well as to support the validity of proxy-based quantitative reconstructions (Battarbee 2000, Birks et al. 2000).

The principal goal of this study was to examine the impacts of long-term changes in climate and post-glacial sea-level rise on the diatom flora of Lake Stowell, a low-elevation coastal lake in southern British Columbia. This lake was chosen due to the comprehensive paleo-

environmental (Heusser et al. 1985, Kienast and McKay 2001, Galloway et al. 2007, Roe et al. 2009, Lucas and Lacourse 2013, Leopold et al. 2016) and sea-level histories (Hutchinson et al. 2004, James et al. 2009, Roe et al. 2013, Shugar et al. 2014, Fedje et al. 2018) available from the region. A previous study of Lake Stowell provides a chironomid-inferred temperature reconstruction at a local scale for the past ~14,200 yr (Lemmen and Lacourse 2018), which is primarily used to examine the overall role of climate in governing diatom flora within the lake.

MATERIALS AND METHODS

Study site

Lake Stowell (48°46.9' N, 123°26.63' W) is located on Saltspring Island, a small island adjacent to Vancouver Island on the south coast of British Columbia, Canada (Fig. 1). The region is characterized by relatively mild temperatures year-round. Mean January and July air temperatures at nearby Cusheon Lake on Saltspring Island are 2.8°C and 16.1°C, respectively, and mean annual precipitation is 1070 mm/yr (Environment Canada 2018). Lake Stowell sits at an elevation of only 70 m asl and is approximately 1.5 km from the modern shoreline. The catchment consists primarily of open *Pseudotsuga menziesii*-dominated forest. Agricultural pasture is located on the northeast side of the lake. The lake has a relatively small surface area (5 ha) and a maximum depth of 7.5 m. In July 2015, lake pH was 7.77, Secchi depth was 2.3 m, and dissolved organic carbon (DOC) was 5.6 mg/L.

Core collection and radiocarbon dating

A 768.5-cm sediment core was collected from Lake Stowell using a Livingstone piston corer from a raft anchored in 7.24 m of water. The uppermost 70 cm of sediment was collected in a clear polycarbonate tube fitted with a piston. The sediment core from Lake Stowell was the focus of a previous study by Lemmen and Lacourse (2018) in which fossil chironomid assemblages were used to infer mean July air temperatures (MJAT) using the transfer function from Fortin et al. (2015). In the Lemmen and Lacourse (2018) study, loss on ignition (LOI) was conducted by drying 1 cm³ sediment samples at 105°C for 20 h, followed by ignition at 550°C for 4 h.

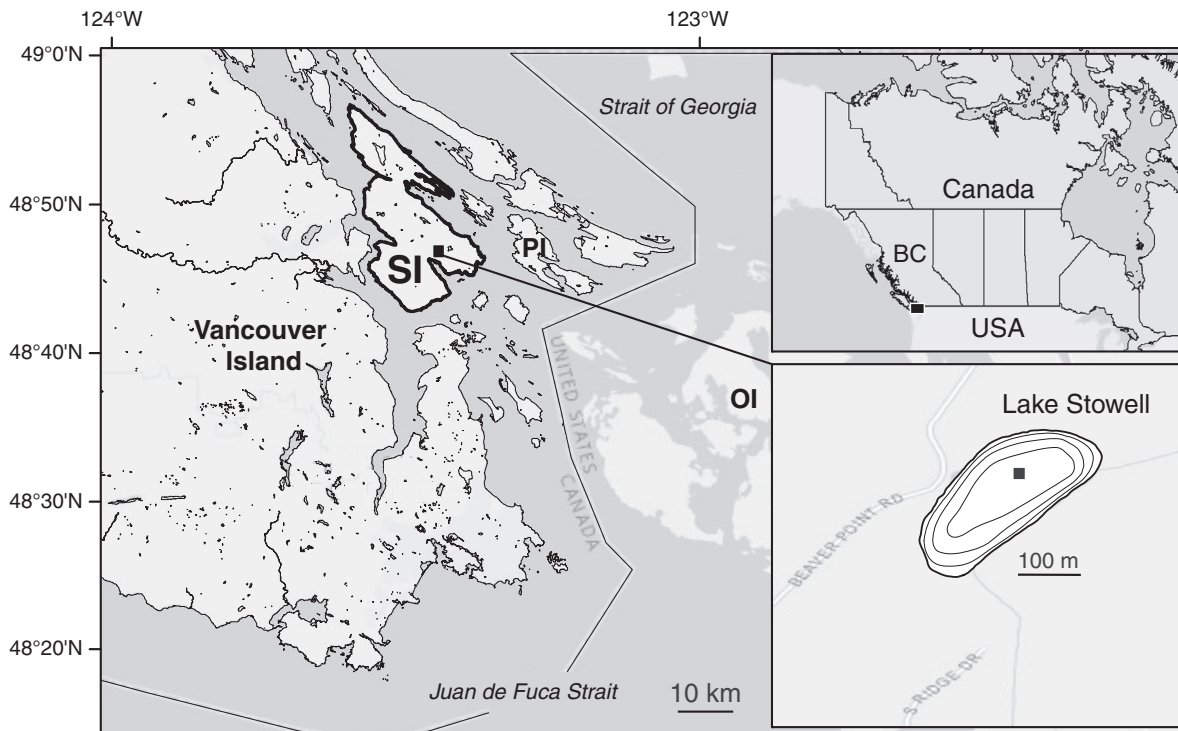


Fig. 1. Map showing the location of Lake Stowell on Saltspring Island (SI), British Columbia. Top inset shows location in northern North America. Bottom inset shows Lake Bathymetry at 2-m depth intervals and the coring location (square). OI, Orcas Island; PI, Pender Island.

Magnetic susceptibility was determined using a Bartington MS2E high-resolution surface scanner. Six AMS radiocarbon ages (Appendix S1: Table S1) were obtained on plant macrofossils and were calibrated to calendar years using the IntCal13 data set (Reimer et al. 2013). A chronology for the core was built using Stineman interpolation (Johannesson et al. 2012) in the clam package (Blaauw 2010) in R (R Core Team 2013) on these six ages, the Mazama tephra (Egan et al. 2015), and an age of -63 cal yr BP for the top of the core (Fig. 2).

Preparation and identification of diatoms

Sediment samples of 0.25 cm^3 were extracted at 2- to 10-cm intervals down the length of the core to a depth of 629 cm and placed into 20-mL glass vials. Standard protocols were followed to prepare the samples for diatom analysis (Battarbee et al. 2001). Hydrogen peroxide (30%) was added to each vial, and the samples were left to digest in an 80°C water bath for 3–4 h. Samples

were then centrifuged at 1200 rpm for 4 min, supernatant liquid was removed by suction, and the samples were rinsed with deionized water; this procedure was repeated several times. To enable the calculation of fossil diatom concentrations and accumulation rates, 1.0 mL of a microsphere suspension with a known concentration (5×10^6 spheres/mL) was added to each sample following digestion and rinsing. Coverslips were prepared by pipetting a diatom slurry from each sample (diluted with deionized water) onto their cleaned surfaces and allowing them to air-dry at room temperature. Coverslips were then permanently mounted on microscope slides using Naphrax.

Diatoms were enumerated with a Nikon 90i microscope (Minato, Tokyo, Japan) at $1000\times$ magnification, under oil immersion, and with differential interference contrast optics. A minimum of 475 valves was identified in each sample using Antoniadis et al. (2008), Siver et al. (2005), Krammer and Lange-Bertalot (1991a, b), and Patrick and Reimer

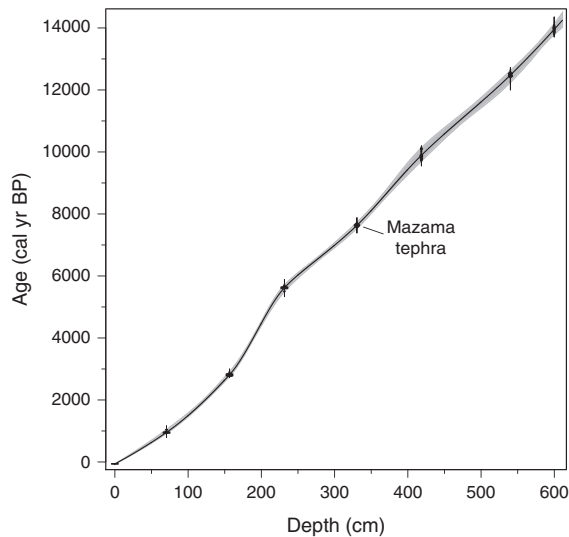


Fig. 2. Age-depth model for the sediment core from Lake Stowell, British Columbia. Gray bands are 95% confidence intervals based on 10,000 iterations of a Stineman interpolation of calendar age probability distributions (Appendix S1: Table S1).

(1966, 1975). A chrysophyte scale-to-diatom valve index was calculated by counting both groups on the prepared slides and following the formula in Karmakar et al. (2015); however, only diatoms were identified to the genus and species level.

Numerical analyses

The diatom data are shown in percentage diagrams. Prominent taxa ($n = 23$) representing $\geq 5\%$ of the total diatom sum in at least two samples (Fig. 3, Table 1), and the category other in which rare species were grouped ($n = 106$), were used in statistical analyses. Of the taxa that were considered rare, 33 fell in the range of $1\% \leq x < 5\%$ (Appendix S1: Fig. S1), and 73 had $\leq 1\%$ relative abundance (individual profiles are not shown). The diatom data were Hellinger transformed (Legendre and Gallagher 2001, Legendre and Birks 2012) prior to statistical analyses, and the variance in the data was summarized with principal component analysis (PCA; Fig. 4) using the vegan package (Oksanen et al. 2008) in R. Diatom percentages were zoned into stratigraphically constrained clusters based on changes in the scores of the first three PCA axes (Fig. 5). An unconstrained cluster analysis was also

performed to assess similarities of diatom communities through time, irrespective of their position in the core. This was done using the rioja package (Juggins 2017) in R, with Euclidean distance and Ward's method as set parameters under the hclust function. The number of significant zones was tested with a broken-stick model (Bennett 1996).

RESULTS

Sediment stratigraphy

The sediment core from Lake Stowell begins in gray marine clay (768.5–604 cm) with magnetic susceptibility in excess of 100 SI below 630 cm. The clay is sharply overlain by light-brown gyttja (604–579 cm) with LOI values of 10–20% and magnetic susceptibility of 2–6 SI (Fig. 5). The remainder of the core (579–0 cm) is composed of dark-brown gyttja with organic matter content that increases from 25% to 50% and magnetic susceptibility near or at 0 SI. Based on the age-depth model (Fig. 2), sedimentation rates for the gyttja are more or less steady along the length of the core at 0.04 cm/cal yr. The model predicts an age of $14,011 \pm 180$ cal yr BP for the transition from marine clay to gyttja, which is consistent with regional sea-level reconstructions (James et al. 2009).

Diatom biostratigraphy

A total of 125 samples were analyzed for diatoms, spanning the past $\sim 14,600$ yr. The stratigraphic diagrams (Fig. 3; Appendix S1: Fig. S1) were divided into six major zones based on changes in PCA scores of the diatom percentages (Figs. 4, 5). The constrained cluster analysis (Fig. 5) showed long-term changes in the diatom assemblages at Lake Stowell (millennial-scale), compared to the unconstrained cluster analysis, which revealed some shorter-term similarities (decadal to century scale). From 14.6 to 8.5 ka, the unconstrained clusters showed clear distinctions of groups that were similar to the PCA-based zones, despite the analysis being unconstrained stratigraphically; this indicates that diatom assemblages over this period most closely resembled those in adjacent samples. In the mid-to late Holocene portion of the Lake Stowell record, particularly from 3.4 ka to present, the unconstrained clusters alternated back and forth

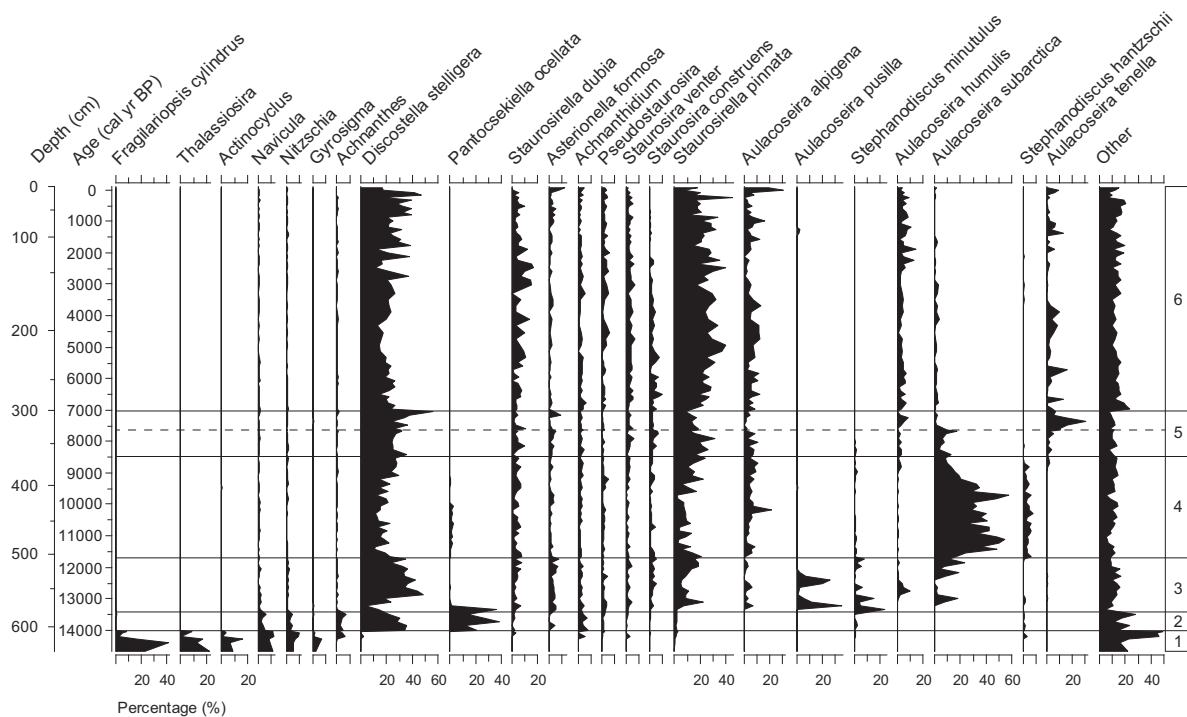


Fig. 3. Diatom biostratigraphy for the Lake Stowell sediment core, expressed as percentages of total abundance. Only the main taxa with $\geq 5\%$ relative abundance in at least one sample are shown. The dashed line in zone 5 represents the stratigraphic position of the Mazama tephra.

between two groups, showing higher variability in the diatom assemblages that coincided with increases in MJAT and with changes in the ratio of benthic/fragilarioid to planktonic diatoms (Fig. 5). Independent zonation of fossil chironomid assemblages from the Lake Stowell sediment core produced nearly identical biostratigraphic zones to the constrained cluster analysis of the diatom data (Fig. 6). The major difference was an additional chironomid zone that started at ~ 3.4 ka, corresponding to the period of higher variability in the diatom assemblages identified by the unconstrained cluster analysis.

Diatom zone 1 (>14.0 ka), in the marine clay portion of the record, was dominated almost entirely by marine taxa, the most abundant of which was *Fragilariopsis cylindrus* representing up to 40% of the total diatom sum (Figs. 3, 7). Taxa such as *Thalassiosira*, *Actinocyclus*, *Navicula*, *Nitzschia*, and *Gyrosigma* had high percentages as well (5–20% each). At ~ 14.2 ka, the ratio of benthic/fragilarioid to planktonic diatom taxa (BF:P) increased nearly threefold and then declined just

as abruptly by the end of the zone. There was an absence of chrysophyte scales relative to diatom valves (CS:DV) until 14.2 ka, after which this ratio increased slightly (Fig. 5).

Zone 2 (14.0–13.4 ka) corresponds with light-brown gyttja overlying the basal marine clays. The zone was marked by the total disappearance of marine diatom taxa, which were replaced by *Discostella stelligera*, *Pantocsekiella ocellata* (each up to 30% of the diatom sum; Figs. 3, 7), and taxa with tolerances for brackish-freshwater conditions (e.g., *Amphora*, *Diploneis*, *Mastogloia*, and *Achnanthes*). The BF:P was low throughout this zone, and the CS:DV was at its highest (i.e., chrysophyte scales were 5–20 \times more abundant than diatom valves).

Zone 3 (13.4–11.7 ka), the beginning of which coincides with a stratigraphic change to dark-brown gyttja, showed increased relative abundances of *D. stelligera*, *Staurosirella pinnata*, *Stephanodiscus minutulus*, and most *Aulacoseira* species, including most notably *Aulacoseira pusilla* (Figs. 3, 7). Taxa that declined in relative

Table 1. Taxon loadings and the explained variance (eigenvalues) of the principal component analysis of fossil diatom assemblages from the Lake Stowell sediment core.

Taxa	Species authority	Taxon code	Components		
			1	2	3
<i>Achnanthes</i>		ACNS	0.45	-0.08	1.12
<i>Achnantheidium</i>		ACTM	-0.48	-0.49	0.85
<i>Actinocyclus</i>		ACTI	1.35	0.44	-0.32
<i>Asterionella formosa</i>	Hassall 1850	A.FORM	-0.59	-0.42	-0.10
<i>Aulacoseira alpigena</i>	(Grunow) Krammer 1991	A.ALPI	-0.82	0.24	-0.58
<i>Aulacoseira humilis</i>	(Cleve-Euler) Genkal & Trifonova 2001	A.HUMI	-0.79	1.01	0.13
<i>Aulacoseira pusilla</i>	(F.Meister) A.Tuji & A.Houk 2004	A.PUSI	-0.02	-0.29	0.08
<i>Aulacoseira subarctica</i>	(O.Müller) E.Y.Haworth 1990	A.SUBA	-0.13	-1.05	-0.82
<i>Aulacoseira tenella</i>	(Nygaard) Simonsen 1979	A.TENE	-0.49	0.78	-0.01
<i>Discostella stelligera</i>	(Cleve & Grunow) Houk & Klee 2004	D.STEL	-1.00	-0.23	0.56
<i>Fragilariopsis cylindrus</i>	(Grunow ex Cleve) Helmcke & Krieger 1954	F.CYLI	1.33	0.45	-0.35
<i>Gyrosigma</i>		GYRO	1.31	0.43	-0.21
<i>Navicula</i>		NAVI	1.33	0.04	0.37
<i>Nitzschia</i>		NITZ	1.24	0.05	0.48
<i>Pantocsekiella ocellata</i>	(Pantocsek) K.T.Kiss & E.Ács 2016	P.OCEL	0.34	-0.89	0.63
<i>Pseudostaurosira</i>		PSEU	-0.58	0.15	0.20
<i>Staurosira construens</i>	Ehrenberg 1843	S.CONS	-0.53	-0.04	-0.07
<i>Staurosira venter</i>	(Ehrenberg) Cleve & J.D.Möller 1879	S.VENT	-0.99	0.56	0.17
<i>Staurosirella dubia</i>	(Grunow) E.A.Morales & K.M.Manoylov 2006	S.DUBI	-0.70	0.24	0.00
<i>Staurosirella pinnata</i>	(Ehrenberg) Williams & Round 1988	S.PINN	-1.06	0.83	-0.05
<i>Stephanodiscus hantzschii</i>	Grunow 1880	S.HANT	0.21	-1.09	-0.51
<i>Stephanodiscus minutulus</i>	(Kützing) Cleve & Möller 1882	S.MINU	0.18	-0.85	0.14
<i>Thalassiosira</i>		THAL	1.34	0.47	-0.36
Other taxa		OTHER	0.84	0.49	0.65
Eigenvalues			0.327	0.151	0.097

abundance included *P. ocellata*, *Navicula*, *Nitzschia*, and several other large benthic taxa. This resulted in a low BF:P for the zone, and at the same time, the CS:DV gradually decreased (Fig. 5).

Zone 4 (11.7–8.5 ka) was dominated by *Aulacoseira subarctica*; this species reached up to 55% of the total diatom sum by ~11.1 ka and decreased after 9.7 ka (Fig. 3). *Stephanodiscus hantzschii* and *Aulacoseira alpigena* increased as well; however, many prominent taxa declined in this zone (e.g., *D. stelligera* and *S. pinnata*). The BF:P was low in this zone, and the CS:DV increased initially before declining again after ~10.0 ka (Fig. 5).

Zone 5 (8.5–7.0 ka) initially showed an increase in *D. stelligera* and *S. pinnata*, and in the BF:P (Figs. 3, 5). The deposition of the Mazama tephra at ~7.6 ka was associated with abrupt increases in *Aulacoseira tenella*, *Aulacoseira humilis*, and *D. stelligera*, as well as brief declines in *S. pinnata*, *A. alpigena*, and the BF:P. The CS:DV remained low throughout the zone.

Zone 6 (7.0 ka–present) had higher relative abundances of *Staurosirella dubia*, *S. pinnata*, and most *Aulacoseira* species (with the exception of *A. subarctica*), and lower abundances of *D. stelligera* (Fig. 3). The BF:P increased gradually at the beginning of the zone (Fig. 5) and peaked at ~2.5 ka, that is, the combined percentage of benthic/fragilarioid taxa was 3.5× greater than that of planktonic taxa. The BF:P declined rapidly from 2.5 to 1.8 ka and gradually after that. As in the previous zone, CS:DV remained low from 7.0 ka to the present.

Principal component analysis

The first three axes of the PCA were statistically significant (Table 1) and explained 58% of the variance in the diatom assemblages of Lake Stowell (Fig. 5; PC1, 33%; PC2, 15%; and PC3, 10%). The first diatom PCA axis likely represents an association with salinity; it was positively loaded on marine and brackish taxa (e.g., *F. cylindrus*, *Thalassiosira*, *Actinocyclus*, and

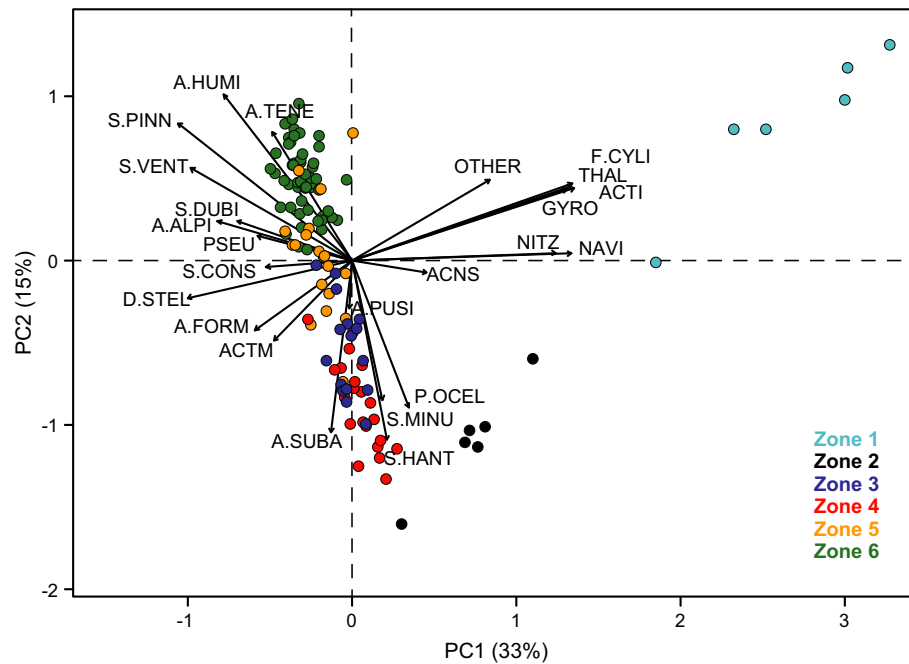


Fig. 4. Biplot of a principal component analysis (PCA) of fossil diatom assemblages from Lake Stowell, British Columbia. Samples are color-coded according to the biostratigraphic zones defined by the diatom PCA axes (Fig. 5). Taxon codes are listed in Table 1.

Gyrosigma), and negatively loaded on taxa typical of freshwater lakes or warm conditions, such as *Aulacoseira* spp. and *D. stelligera*, respectively (Fig. 4). This axis had large positive scores in zone 1 (14.6–14.0 ka) and zone 2 (14.0–13.4 ka), relatively neutral scores in zone 3 (13.4–11.7 ka) and zone 4 (11.7–8.5 ka), and slightly negative scores in zone 5 (8.5–7.0 ka) and zone 6 (7.0 ka–present) (Fig. 5).

The second PC axis could be related to lake water depth; it was positively loaded on many of the small fragilarioids and larger benthic diatoms, such as *S. pinnata*, *Staurosira venter*, and *Gyrosigma*, as well as the other category primarily comprised of benthic taxa (e.g., *Brachysira*, *Gomphonema*, *Psammothidium*, *Planothidium*, and *Rossithidium*). This axis was also negatively loaded on planktonic taxa such as *A. subarctica*, *P. ocellata*, *D. stelligera*, *S. hantzschii*, *S. minutulus*, and *Asterionella formosa*, with a few exceptions (*A. humilis* and *A. tenella* were positively loaded on this axis). This axis had positive scores in the lowermost and uppermost zones (1, 5, and 6), and negative scores in the middle zones (2, 3, and 4).

The third PC axis is likely associated with lake nutrient concentrations; it was positively loaded on taxa with higher optima for nitrogen and/or phosphorus (e.g., *D. stelligera*, *P. ocellata*, *Achnanthes*, *Achnantheidium*), and negatively loaded on taxa with lower tolerances for nutrient-rich waters, such as *A. subarctica*. The third axis mostly separates the negative scores in zones 1 and 4 from the large positive scores in zone 2.

DISCUSSION

Sea-level history and isolation of Lake Stowell

The beginning of the Lake Stowell sediment record corresponds with the Bølling/Ållerød interstadial (14,640–12,850 cal yr BP; Kuehn et al. 2014), which was a period marked by global-scale warming and regional-scale RSL changes following deglaciation of the Cordilleran Ice Sheet (Cosma et al. 2008, James et al. 2009). The Juan de Fuca Lobe of the ice sheet overlying southern Vancouver Island began its retreat earlier at ~17,500 cal yr BP, and low elevations were ice-free by ~15,500 cal yr BP (Barrie and Conway 2002, Mosher and Hewitt 2004). At ~14,350 cal yr

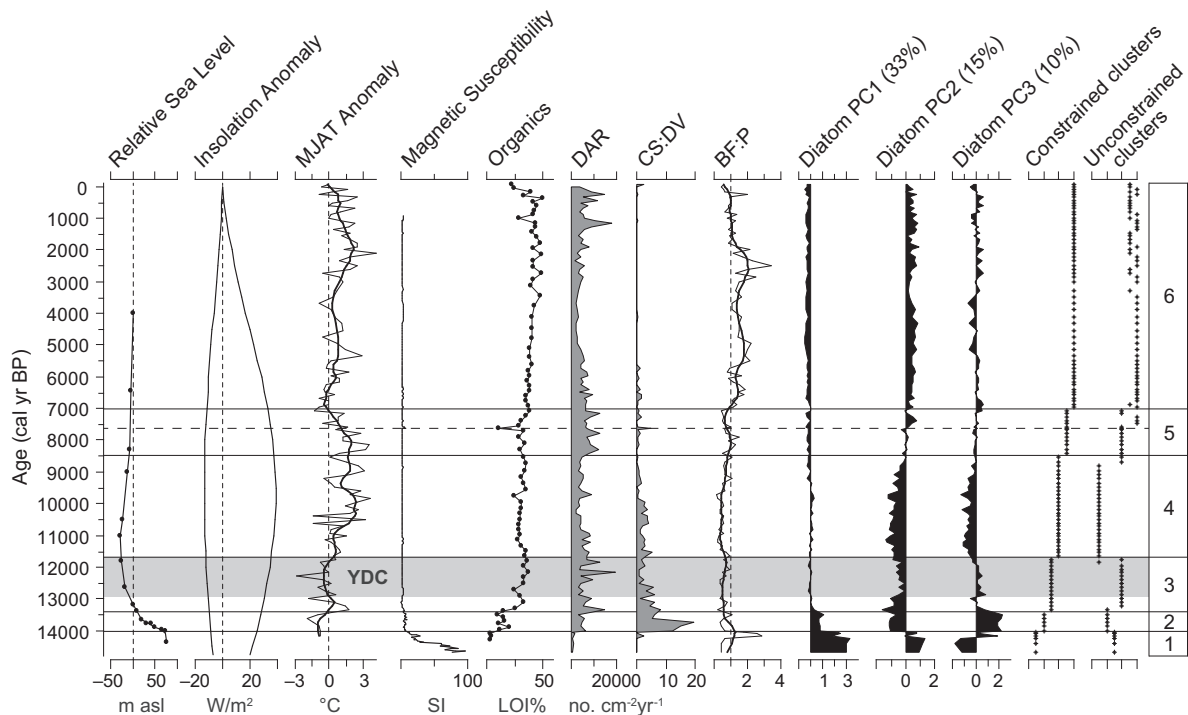


Fig. 5. A paleo-environmental summary for Lake Stowell, British Columbia, including chironomid-inferred mean July air temperature (MJAT) anomalies, magnetic susceptibility, and organic content from Lemmen and Lacourse (2018). Relative sea level (m asl) represents the “preferred curve” from James et al. (2009). January and July insolation anomalies at 47.5° N are from Berger and Loutre (1991). Dashed line in zone 5 shows the stratigraphic position of the Mazama tephra. DAR, diatom accumulation rate; CS:DV, chrysophyte scale-to-diatom valve ratio; BF:P, benthic/fragilarioid-to-planktonic diatom ratio; YDC, Younger Dryas chronozone.

BP, RSL on the south coast of British Columbia was at a high stand of +75 m elevation (James et al. 2009); however, glacio-isostatic rebound following ice withdrawal caused rapid changes in RSL, which in turn affected ontological processes of lakes within the region. Relative sea level fell below the height of the present shoreline by ~13,200 cal yr BP and reached a low stand of up to –30 m at 11,000 cal yr BP (James et al. 2009, Shugar et al. 2014). Lake basins in the region including that of Lake Stowell became isolated from saline waters as RSL decreased (Hutchinson et al. 2004, Roe et al. 2013, Fedje et al. 2018). The precise timing of these events at a local scale can be inferred from sediment records by identifying marine-to-freshwater transitions in diatom assemblages.

Clay at the base of the Lake Stowell sediment core reflects sedimentation in what was a near-shore marine environment following ice retreat

and subsequent decreases in RSL (James et al. 2009). Before 14.0 ka, diatom assemblages at Lake Stowell were primarily comprised of marine taxa (Fig. 7) with preferences for high salinity, including *F. cylindrus*, *Thalassiosira*, *Cocconeis costata*, and *Tryblionella* (Lortie 1983, van Dam et al. 1994, Pienitz et al. 2003, Fedje et al. 2018, Guiry and Guiry 2019). These taxa disappeared abruptly by 14.0 ka, indicating that the basin became isolated as RSL fell below +70 m (James et al. 2009). After 14.0 ka, isolation of the basin was marked by the deposition of light-brown gyttja otop of marine clay. *Pantocsekiella ocellata* and *D. stelligera* increased in abundance to become the dominant taxa in the record (~50% of the total diatom sum), suggesting that salinity had dropped below 0.9‰ (van Dam et al. 1994, Wilson et al. 1996). The corresponding and rapid increase in chrysophyte scales relative to diatom valves (CS:DV) supports the

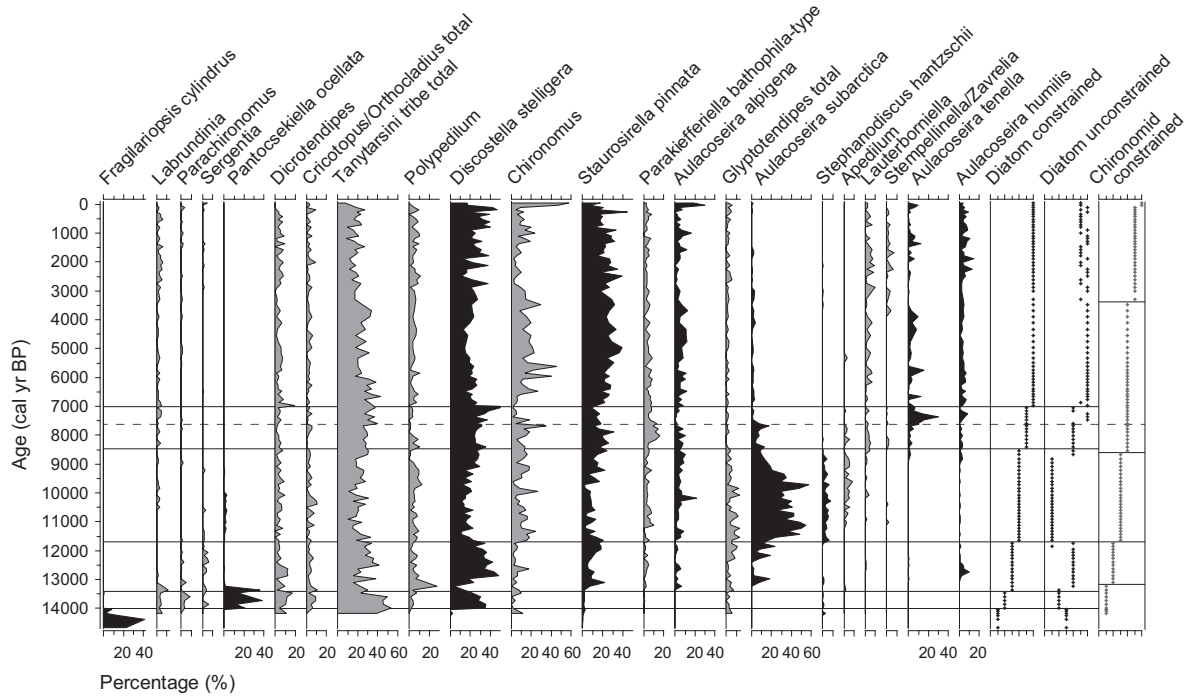


Fig. 6. Relative abundances of select diatoms (black) and chironomids (gray; Lemmen and Lacourse 2018) from Lake Stowell, British Columbia. Solid horizontal lines show constrained diatom zones based on biostratigraphic changes in the diatom assemblages. Chironomid zones based on biostratigraphic changes in fossil midge assemblages are shown on the far right. Dashed horizontal line shows the stratigraphic position of the Mazama tephra.

inference of declining salinity, as chrysophytes in general are abundant only in freshwaters (Cumming et al. 1993). Isolation of the Lake Stowell basin is consistent in terms of timing with other diatom studies around Vancouver Island, which describe rapid declines in marine or polyhalobian taxa associated with RSL withdrawal at ~14.0 ka (Hutchinson et al. 2004, James et al. 2009, Roe et al. 2013, Fedje et al. 2018).

At ~14.2 ka, before the complete disappearance of marine taxa in the Lake Stowell record, there was an increase in taxa such as *Ctenophora*, *Mastogloia*, *Diploneis*, and *Amphora* (Fig. 7) that are tolerant of brackish environments with moderate salinity levels (van Dam et al. 1994, Wilson et al. 1996, Pienitz et al. 2003, Fedje et al. 2018). Relative abundances of these species collectively reached up to 25% of the total diatom sum for ~800 yr until 13.4 ka, during which time RSL dropped from +75 m to +10 m elevation (James

et al. 2009). At low-elevation lagoonal sites on Lasqueti Island, further north along the coast, Hutchinson et al. (2004) attributed similarly timed transitions in diatom assemblages to slow rates of crustal rebound following ice retreat. Similar gradual uplift may have occurred at Lake Stowell; however, given its elevation at 70 m asl, it is possible that an influx of clastic materials was instead responsible for triggering an increase in benthic diatoms (Hickman and Reasoner 1994), which could also be described as tolerant of brackish-to-freshwater conditions. This interpretation is supported by high values of magnetic susceptibility in the early record of Lake Stowell (Fig. 5), as well as a peak in benthic diatoms (BF:P; Fig. 5) at 14.2 ka.

The chironomid record from Lake Stowell begins during this brackish-to-freshwater phase; clays that accumulated in the preceding near-shore marine setting were more or less barren of midge remains (Lemmen and Lacourse 2018).

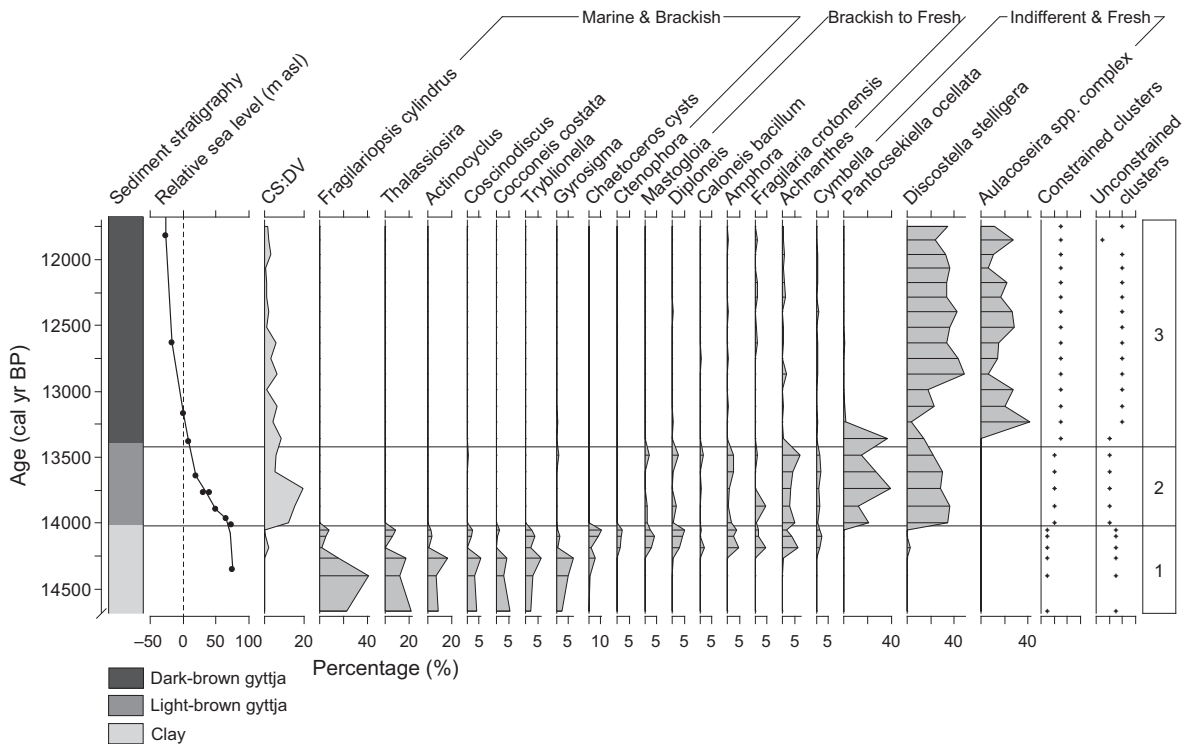


Fig. 7. Diatom percentages of select species corresponding to the marine-brackish-freshwater transition at Lake Stowell. Taxa are grouped by salinity preferences using Lortie (1983), van Dam et al. (1994), Pienitz et al. (2003), Fedje et al. (2018), and Guiry and Guiry (2019). Note changes in scale on the x-axes. Relative sea level (m asl) represents the “preferred curve” from James et al. (2009). Lake Stowell is located at 70 m asl. CS:DV, chrysophyte scale-to-diatom valve ratio.

Chironomid assemblages between 14.2 and 13.4 ka include of an array of taxa, but consist primarily of Tanytarsini, *Dicrotendipes* and *Poly-pedilum* (Fig. 6), which are typical of freshwater lakes but can tolerate low-to-moderate salinities (Walker et al. 1995, Heinrichs and Walker 2006, Dickson et al. 2014). *Cricotopus/Orthocladius* accounts for up to 11% of the chironomid assemblages during the transition from brackish-to-freshwater conditions. As with the other chironomid taxa present during this interval, *Cricotopus/Orthocladius* is found across a broad range of salinities; however, it can also dominate saline lakes to the exclusion of all other taxa (Walker et al. 1995, Zhang et al. 2007), making it one of only a few chironomid taxa that can be considered halophilic. The chironomid assemblages during this early phase of Lake Stowell are therefore consistent with the diatom record, which reflects a newly isolated lake basin with evidence

for somewhat brackish conditions after the transition from a nearshore marine environment at ~14 ka.

After 13.4 ka, sediment accumulation in the Lake Stowell basin consisted of dark-brown gyttja with relatively high organic matter content. Diatom assemblages showed large increases in freshwater taxa (Figs. 3, 7) with optima for low salinity levels (<0.2‰) such as those in the *Aulacoseira* spp. complex (Lortie 1983, van Dam et al. 1994, Wilson et al. 1996, Fedje et al. 2018), which had previously been absent from the record. Formation of the newly isolated, freshwater basin was therefore coincident with warming toward the end of the Bølling/Ållerød Interstadial (Kuehn et al. 2014). At this time, an increase in diatom accumulation rates (DAR; Fig. 5; Appendix S1: Fig. S2) and a decline in chrysophyte scales relative to diatom valves (CS:DV) signaled increased primary productivity, perhaps

due to increasingly longer growing/blooming seasons (Smol 1985).

Diatom responses to Holocene environmental change

Prior to the onset of the Holocene (~11,700 cal yr BP), chironomid-inferred MJAT at Lake Stowell was relatively cool, that is, up to 3°C cooler than modern (Lemmen and Lacourse 2018), though there was an overall trend of warming associated with the near end of the Bølling/Ållerød Interstadial (Kuehn et al. 2014). Brief increases in several warm-associated chironomid taxa, such as *Labrundinia* and *Glyptotendipes*, were associated with a rise in MJAT from 14.0 to 13.0 ka (Figs. 5, 6). Diatom assemblages showed simultaneous increases in planktonic *D. stelligera* and *P. ocellata*, also indicative of warming climatic conditions and thermal stability in the lake (Rühland et al. 2003, Voit et al. 2014).

Subsequent cooling at the beginning of the Younger Dryas chronozone (YDC; ~12,900–11,700 cal yr BP) prompted subtle responses in terrestrial and aquatic biota across coastal British Columbia (Mathewes 1993, Lacourse 2005, Lemmen and Lacourse 2018). At Lake Stowell, chironomids with preferences for cooler temperatures (e.g., *Sergentia*) increased in abundance (Lemmen and Lacourse 2018), closely paralleling shifts captured in the diatom record. For instance, slight increases in cool-adapted, alkaliphilous taxa (e.g., *S. pinnata*, *Staurosira construens*, and *S. dubia*) at the expense of *D. stelligera* and *P. ocellata* could be interpreted as a response to lowering temperatures, as well as elevated lake pH related to enhanced weathering in the late-glacial period (Paull et al. 2008, Voit et al. 2014). The changes in diatom assemblages were similar in overall nature and timing to those occurring at Two Frog Lake, located northeast of Vancouver Island, which were likewise attributed to cooling in the YDC (Galloway et al. 2007).

Intermittent increases in several *Aulacoseira* spp. (Fig. 3) at Lake Stowell during the YDC suggest that cooling may have weakened lake thermal stratification, leading to turbulent conditions that favored taxa with heavily silicified valves (Rühland et al. 2003, 2015). Diatom assemblages were thus influenced by the direct and indirect aspects of a cooling climate, and also appeared to respond to increased nutrient concentrations;

there were increases in taxa indicative of nutrient enrichment, such as *Aulacoseira* spp. and *A. formosa* (Wolin and Stoermer 2005, Neil and Gajewski 2017), as well as those with requirements for relatively high total phosphorus, such as *A. pusilla*, *S. minutulus*, and *S. pinnata* (Enache and Prairie 2002, Cumming et al. 2015, Estep and Reavie 2015). Finally, there was an increase in total DAR (Fig. 5), signaling higher primary productivity.

In the early Holocene, high summer insolation from ~11,700 to 8000 cal yr BP led to rising summer temperatures throughout much of the Northern Hemisphere, including coastal British Columbia (Heusser et al. 1985, Kienast and McKay 2001, Lemmen and Lacourse 2018). At Lake Stowell, warm-associated chironomid taxa increased during this period (e.g., *Labrundinia*, *Glyptotendipes*, *Apedilum*, and *Pseudochironomus*; Lemmen and Lacourse 2018). Changes in Lake Stowell diatom assemblages were not as clearly associated with direct influences of summer insolation and/or temperature; for instance, *A. subarctica* is a cold-water species (Nieminen 2008) that increased significantly in the early Holocene, in contrast with many proxy records from the region that infer warming during this period. This suggests that this species was instead responding to another aspect of climate or an independent forcing (Solovieva et al. 2015), such as reduced nutrients from the surrounding catchment (Galloway et al. 2007, Bennion et al. 2012), or perhaps a prolonged period of vigorous mixing within the water column (Kienel et al. 2005, Horn et al. 2011, Roe et al. 2013). Gibson et al. (2003) suggest that *A. subarctica* is a better competitor under low total phosphorus (TP) concentrations compared to *Stephanodiscus* spp., which often replace it as TP increases. In the early Holocene at Lake Stowell, *A. subarctica* was 7–10× more abundant than *S. hantzschii* and total DAR was decreasing, indicating limited productivity that was perhaps caused by lower inputs of external nutrients to the lake.

Regional landscape cover may have also played an important role in governing aquatic biota at Lake Stowell. In the early Holocene, pollen assemblages from Roe Lake on nearby Pender Island (10 km east of Lake Stowell) were dominated by high relative abundances of *P. menziesii*, Poaceae, and *Pteridium aquilinum*,

indicating an open forest canopy comprised of Douglas fir-grass-fern communities (Lucas and Lacourse 2013). Similar changes were observed in plant communities on nearby Orcas Island (Leopold et al. 2016) and in a marine pollen record from nearby Saanich Inlet (Pellatt et al. 2001). At Lake Stowell, an open forest canopy would have rendered the lake more susceptible to mixing due to a lack of protection from wind, thereby favoring taxa such as *A. alpigena*, *A. subarctica*, and *S. hantzschii*. These planktonics have heavily silicified valves that would have required turbulent conditions to keep them suspended in the upper water column (Galloway et al. 2007, Rühland et al. 2015), as well as high requirements for silica, which may have been reintroduced from the lake bottom upon more vigorous mixing (Wolfe 1996, Hausmann et al. 2011).

Summer temperatures in coastal British Columbia began to decrease after ~8000 cal yr BP, leading to a generally cooler climate in the mid- and late Holocene (Heusser et al. 1985, Kienast and McKay 2001, Lemmen and Lacourse 2018). At 7600 cal yr BP, the volcanic eruption of Mount Mazama in Oregon (Egan et al. 2015) resulted in widespread deposition of tephra that extended northward to southern British Columbia. The deposition of Mazama tephra appears to have had a weak effect on chironomid assemblages at Lake Stowell (Lemmen and Lacourse 2018); only a few chironomid taxa showed changes immediately following the tephra deposition, for example, decreases in *Parakiefferiella* and *Chironomus* (Fig. 6). Diatom responses to tephra deposition vary greatly between lakes, but they are often described as short-lived and linked to mass influxes of particulate silica (Si) that stimulate the productivity of siliceous algae (Telford et al. 2004). Primary productivity inferred from total DAR at Lake Stowell did not show significant changes following deposition of the Mazama tephra; however, there were brief increases in individual taxa, most notably *A. tenella* and to a lesser extent *A. humilis* and *D. stelligera* (Fig. 3). These particular taxa have been shown to respond to tephra deposition, high Si:P ratios (Saros et al. 2005, Egan et al. 2019), and/or nutrient enrichment (Fritz and Anderson 2013, Neil and Gajewski 2017), which were likely consequences of the Mazama tephra deposition. Michelutti et al. (2016) suggest that

tephra deposition also reduces the availability of benthic or epiphytic habitats in lakes through decreased light penetration and the destruction of aquatic macrophytes. Immediately following deposition of the Mazama tephra at Lake Stowell, CS:DV showed a brief peak and BF:P decreased (Fig. 5) before quickly recovering by 7.0 ka, potentially reflecting an interval when the environment was more suitable for chrysophytes and/or planktonic diatom taxa. To achieve a more robust assessment of the effects of tephra on lake aquatic biota at this site, further analyses of both chironomid and diatom assemblages would be needed at a higher temporal resolution.

In the mid- to late Holocene, decreasing summer insolation led to cooler temperatures (Walker and Pellatt 2003, Lemmen and Lacourse 2018), though changes were subtle relative to those of the late-glacial and the early Holocene. Lake Stowell diatom assemblages showed a broad increase in the cool-adapted *S. pinnata* over the typically warm-associated *D. stelligera* (Rühland et al. 2003) until ~3.0 ka, supporting chironomid-inferred cooling relative to the early Holocene (Lemmen and Lacourse 2018). Increased abundances of *A. alpigena*, *A. humilis*, and *A. tenella* from 7600 cal yr BP to the present could indicate biogeochemical coupling of terrestrial succession and limnological conditions, as these taxa are often linked with high DOC and/or humic-stained waters (Haig et al. 2013). Engstrom et al. (2000) demonstrate that lakes are sensitive to vegetation and soil changes in the surrounding catchment and can show stratigraphic patterns consistent with the gradual accumulation of DOC over time, which is supported by the slow increase in organic content in Lake Stowell sediments (Fig. 5). Pollen records from sites near Lake Stowell (Pellatt et al. 2001, Lucas and Lacourse 2013, Leopold et al. 2016) showed expansions of *Quercus garryana* and *P. menziesii*, particularly between 7600 and 5500 cal yr BP. This oak savannah/woodland could be related to increased fire frequency during this period. Diatom taxa such as *A. humilis* have been shown to increase in response to ash deposition following fire events (Enache and Prairie 2000); this species increased at Lake Stowell during the period of oak savannah/woodland expansion (Appendix S1: Fig. S2), again

suggesting a possible association with landscape disturbances and/or vegetation composition in the catchment.

Throughout the Holocene, major shifts in climate and aquatic assemblages are recorded at centennial to millennial scales. Ecosystem responses to increased human activities over the last 100 yr are only captured in the uppermost 2–3 samples of the Lake Stowell record. A substantial increase in *Chironomus* head capsules in the uppermost sediments can be linked to recent anthropogenic influences on the lake and surrounding watershed (Lemmen and Lacourse 2018). Similarly, an increase in certain diatom species (e.g., *A. alpigena* and *A. formosa*) signals greater nutrient input to the lake as a result of nearby anthropogenic activities (Wolin and Storer 2005, Yang et al. 2008, Cumming et al. 2015).

CONCLUSION

Fossil diatom assemblages at Lake Stowell were associated with several external forcings, including (1) post-glacial sea-level changes, (2) both direct and indirect aspects of climate, for example, variations in summer insolation/temperature, lake thermal stratification, and vegetation succession in the surrounding catchment, and (3) natural and anthropogenic disturbances.

Toward the end of the late-glacial period, a transition from marine-to-freshwater diatom assemblages (from 14.2 to 13.4 ka) marked the isolation of the Lake Stowell basin. The consistency of this timing with other sea-level histories from the region (Hutchinson et al. 2004, James et al. 2009, Roe et al. 2013, Fedje et al. 2018) indicates that this diatom record could serve as a reliable indicator of paleo-salinity.

Prior to and throughout the Holocene, shifts in diatom assemblages at Lake Stowell were largely driven by fluctuations in chironomid-inferred climate, as well as vegetation succession in the surrounding catchment, by extension. For instance, Younger Dryas cooling (12.9–11.7 ka) was linked with increases in cold-adapted diatom taxa, and an opening in the forest canopy in the early Holocene (11.7–8.0 ka) likely allowed for higher abundances of heavily silicified taxa as a result of vigorous lake mixing. Mid- to late Holocene

increases in taxa indicative of higher DOC and/or humic-stained waters also indicated potential biogeochemical coupling of terrestrial succession and limnological conditions. Biostratigraphic changes in diatom communities closely matched those of chironomids extracted from the same lake sediments (Lemmen and Lacourse 2018), demonstrating a future avenue for work with respect to comparisons of quantitative reconstructions using both proxies.

Climate had an overarching, long-term influence on diatom assemblages at Lake Stowell through both direct and indirect pathways; however, disturbances on the landscape also had consequences for the trophic status of the lake. Deposition of Mazama tephra at 7.6 ka would have resulted in increased turbidity, nutrient enrichment, a higher Si:P ratio, and a decrease in benthic habitats, which impacted the diatom assemblages. Similarly, changes in diatom and chironomid assemblages over the last 100 yr suggest greater nutrient input to the lake as a result of nearby anthropogenic activities. Analyses at higher temporal resolutions are needed to better assess the impacts of tephra deposition and recent human activities on this low elevation, coastal lake ecosystem.

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