DYNAMICS OF PHYTOPLANKTON DISTRIBUTION IN RELATION TO STRATIFICATION AND WINTER PRECIPITATION, FALLEN LEAF LAKE, CALIFORNIA

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ABSTRACT.—Seasonal succession and interannual variation of modern diatom populations in Fallen Leaf Lake, Sierra Nevada, California, are characterized and discussed in relation to stratification, water quality, and inflow during spring runoff. Fallen Leaf Lake is a deep, transparent subalpine lake that undergoes a 5–6 month period of stratification and develops a deep chlorophyll maximum (DCM) dominated by diatoms. A seasonal succession was observed, where the early spring was dominated by *Asterionella formosa*, *Fragilaria tenera*-group (*F. tenera* and *F. nanana*), *Tabellaria flocculosa* strain IIIp, *Aulacoseira subarctica*, and *Urosolenia eriensis*. *Asterionella formosa* and *T. flocculosa* strain IIIp persisted into the summer, becoming dominant components of the DCM. In late summer, *Cyclotella rossii* succeeded the araphids in the DCM and persisted until deep mixing in the late fall. In winter, the lake is ice free and well mixed, and *Au. subarctica* was abundant in surface waters, along with *Nitzschia* and the other components of the spring bloom. Strong species partitioning occurred between the epilimnion and hypolimnion, and *Handmannia bodanica* was the dominant summer epilimnetic diatom in all years. During a 3-year period, we observed interannual variation in the species of dominant phytoplankton. These years also varied in the depth and development of stratification, development of snowpack in the watershed, and timing of spring melt. The maximum depth of the epilimnion ranged from 12.5 to 17.5 m, and the DCM varied from 30 to 40 m deep. The weakest epilimnetic development was associated with 2011, a year with unusually deep snowpack, wintery spring conditions, and late melting. During 2011, *Fragilaria tenera*-group dominated the phytoplankton, and water clarity was low. A considerable portion of dead lotic diatoms were suspended in the water column, washed in from higher in the watershed during spring runoff. The lotic fraction is a significant portion of surface sediments and may be a useful proxy for identifying past changes in inflow. In addition, ratios of *H. bodanica* and *C. rossii* are explored as a possible proxy for strength in stratification. Collectively, these data provide a solid picture of the seasonal and interannual dynamics of the modern lake system, an essential step in evaluating the climate potential of the diatom record, which is currently being analyzed from lake cores.

RESUMEN.—La sucesión estacional y la variación interanual de las poblaciones modernas de diatomeas en *Fallen Leaf Lake*, Sierra Nevada, California, se describen y caracterizan en relación a la estratificación, la calidad del agua y la afluencia durante la escorrentía de primavera. *Fallen Leaf Lake* es un lago profundo, subalpino y transparente que pasa por un período de estratificación de entre 5 y 6 meses, y desarrolla un máximo profundo de clorofila (DCM) en el que predominan las diatomeas. Se observó una sucesión estacional en donde durante la primera etapa de la primavera predominó la especie *Asterionella formosa*, el grupo *Fragilaria tenera* (*F. tenera* y *F. nanana*), *Tabellaria flocculosa* de la variedad *strain IIIp*, *Aulacoseira subarctica* y *Urosolenia eriensis*. *Asterionella formosa* y *T. flocculosa* de la variedad *strain IIIp* permanecieron durante el verano y fueron los componentes principales del DCM. En la última etapa del verano, *Cyclotella rossii* reemplazó a *araphids* en el DCM y persistió hasta la dilución en aguas profundas al finalizar el otoño. En el invierno, el lago no tiene hielo y la dilución es completa, se encontró gran abundancia de *Au. subarctica* en las aguas superficiales, junto con *Nitzschia* y los demás componentes característicos del inicio de la primavera. La división más desarrollada de especies se produjo entre el *epilimnion* (parte superior más cálida) y el *hypolimnion* (parte más fría), y *Handmannia bodanica* fue la diatomea predominante del verano en el *epilimnion* en todos los años. Durante un período de tres años, observamos la variación interanual en la especie del fitoplancton predominante. A lo largo de estos años también variaron la profundidad y el desarrollo de la estratificación, la acumulación de nieve en la cuenca y el momento del deshielo en primavera. Se observó que la máxima profundidad del *epilimnion* oscilaba entre 12.5 y 17.5 m, y el DCM varió entre 30 y 40 m. de profundidad. El desarrollo más débil del *epilimnion* se registró en el año 2011, cuando se produjeron fenómenos poco habituales: gran acumulación de nieve, temperatura invernal en primavera y deshielo tardío. Durante el 2011, el grupo *Fragilaria tenera* predominó en el fitoplancton y el agua se enturbió. Se encontró una cantidad considerable de diatomeas de agua dulce muertas suspendidas en la columna de agua, provenientes de la cuenca durante la escorrentía de primavera. La fracción lótica de agua es una cantidad significativa de sedimentos que se acumulan en la superficie y puede ser un indicador útil para identificar cambios anteriores en la afluencia de agua. Además, se estudió la relación entre *H. bodanica* y *C. rossii* como un posible indicador de la fuerza de estratificación. En términos generales, se puede decir que esta información brinda una idea clara de la dinámica estacional e interanual del sistema moderno de lagos, lo cual es un paso fundamental para evaluar el potencial del clima para el registro de diatomeas, que en la actualidad, se está analizando a través de material extraído del núcleo del lago.

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Seasonal and vertical distributions of phytoplankton in deep subalpine temperate lakes are known to follow predictable patterns influenced largely by physical structure and nutrient availability (Reynolds 1980, 1984, Sommer 1985). Interannual variations in the strength and onset of these patterns, as well as variations in the dominant taxa, are of particular interest because they form the basis for interpreting diatom-based paleoclimate records in these lake systems. A limnological monitoring program was established in Fallen Leaf Lake, Sierra Nevada, California, with the goal of providing baseline data on the ambient phytoplankton community, including vertical and temporal distribution, for ongoing paleolimnological research. Fallen Leaf Lake is a deep suboligotrophic lake in the Tahoe watershed that has become the subject of research focus because of its strong potential for producing a high-quality paleolimnological record for the Holocene. Previous limnological studies have provided snapshots of the water quality and phytoplankton in the 1970s through the early 1990s (Goldman 1970, Fuller 1975, Goldman et al. 1983, Reuter et al. 1990, 1993, 1996), but these studies were short-lived and did not explore the differential distribution of taxa throughout the water column, particularly in response to seasonal succession, stratification, and nutrient distribution. The objective of this study was to delineate the seasonal and vertical distribution of diatom phytoplankton in Fallen Leaf Lake as an initial step in interpreting the sedimentary diatom record in cores taken for paleoclimate studies. We present data collected over a 3-year period in 2009–2012 and discuss these data in relation to physiological properties, attendant water quality data, and interannual variation in winter precipitation and spring weather conditions. We use the enumeration of diatoms at discrete depths in the water column combined with comparisons to vertical composite plankton tows to discern strong partitioning in response to stratification, and we examine how partitioning may influence the relative abundance of species exported to the sedimentary record.

METHODS

Location

Fallen Leaf Lake is a temperate subalpine lake (1950 m asl) that is 50 m above Lake

Tahoe (Fig. 1). Located at the base of the Glen Alpine glacial valley, Fallen Leaf Lake is dammed at its northern end by a series of recessional moraines (Brothers et al. 2009). The lake basin is steep-sided on all but the northern end, and the littoral zones are sandy with no visually apparent large masses of periphyton. The lake has a maximum depth of 120 m, a mean depth of 70 m, and a surface area of 5.2 km². The watershed (42 km²) is approximately 8 times larger than the lake's surface area, and roughly 80% of the input is derived from snowpack (Hanes 1981). Inflow is principally through Glen Alpine Creek at the southern end of the lake. Outflow occurs at the northwest end of the lake through Taylor Creek and subsurface flow through porous moraines. Outflow then drains into the south end of Lake Tahoe (Kleppe 2005).

Field Methods

Physical, chemical, and biological characteristics were measured on a monthly basis in 2009 (1 June–10 November) and on a seasonal basis in 2010 (1 July, 10 September) and 2011 (21 June, 2 September). Physical measurements included clarity measured with a 20 cm diameter white Secchi disc, as well as thermal and chemical profiles (temperature, dissolved oxygen, conductivity) measured with a YSI-85 for all sample periods. Water for chemical analysis and plankton identification/enumeration was sampled from the epilimnion and the hypolimnion at 12 discrete depths (0, 3, 5, 7.5, 10, 12.5, 15, 17.5, 20, 25, 40, and 50 m) by use of a 2-L Van Dorn sampler. pH was measured to 4 m on 27 July 2009, and alkalinity at selected depths was measured on 27 July 2009 and 28 August 2009 in the field with a Hach titration kit (Table 1). We obtained both surface and vertical phytoplankton tows by using a 15 cm diameter, 20 μ m mesh net, with the vertical tow sampling from 70 m depth to the surface. We sampled the upper 20–30 cm of the lake by using surface tows, wherein we dragged the net behind a boat for approximately 100 m, with the mouth of the net positioned a few centimeters below the water surface. An additional surface plankton tow was taken on 24 April 2009 during our initial reconnaissance of the lake, and the results provided useful early-season data. Also, an unusually dry December made it possible to conduct a vertical plankton tow in January 2012.

Fig. 1. Map of Fallen Leaf Lake, Sierra Nevada, California. A rectangle marks the monitoring station, located over the deepest part of the lake (120 m deep).

Laboratory Analyses

Water samples were cooled and processed within 3 h of collection for algal biomass, nutrients, and phytoplankton identification/enumeration. Algal biomass and degraded algal biomass were determined by measuring chlorophyll *a* and pheophytin pigment concentrations from 100 mL of water. Concentrations were determined via fluorometry (Turner Designs model 10AU Fluorometer) using the Welschmeyer (1994) method with methanol as the solvent. This method was calibrated with purchased standards (chlorophyll *a* from *Anacystis nidulans*, Sigma Corp.), which were calibrated against a spectrophotometric method

(Parsons et al. 1984) for quality assurance. Macronutrients were measured using standard methods (American Public Health Association 2006; total and dissolved phosphorus—USEPA method 365.3; soluble reactive phosphorus—SM4500-PE; nitrate—USEPA method 353.1; ammonia/ammonium—USEPA method 350.1). A subset of samples was analyzed for total Kjeldahl nitrogen (TKN) during 5 of the sampling periods in 2009 (1 June–25 September) by High Sierra Water Lab following USEPA method 351.2 (Table 1). Major cations were analyzed for the first 3 of the 2009 sampling periods (1 June–27 July). Samples for cations were filtered and acidified, then analyzed by Laser Ablation Inductively Coupled Mass

TABLE 1. Measurements of water properties and selected mean water quality values acquired from monthly sampling in 2009 and 2010 at Fallen Leaf Lake, California. For alkalinity values, total alkalinity = HCO_3^- alkalinity. Alkalinity and TKN were measured in the eli-, meta-, and hypolimnion (depths in parentheses). For nutrients and chlorophyll *a*, mean monthly values were determined by averaging values taken from 12 depths at 0, 3, 5, 7.5, 10, 12.5, 15, 17.5, 20, 25, 40, and 50 m.

Date	Secchi (m)	pH	Alkalinity (mg · L ⁻¹)	Chl <i>a</i> (μg · L ⁻¹)	TP (ppb)	DP (ppb)	SRP (ppb)	NO ₃ (ppb)	NH ₄ (ppb)	DIN (ppb)	DIN:DP	TKN
1 Jun 2009	13.3	—	—	—	7	5	1	3	3	6	1.26	58 (5 m) 60 (12.5 m) 52 (25 m)
26 Jun 2009	11.4	—	—	0.45	13	8	2	6	10	15	1.87	64 (0 m) 44 (12.5 m) 64 (25 m)
27 Jul 2009	15.2	7.3	10 (3 m) 9 (17.5 m) 8 (40 m) 7 (3 m)	0.42	13	10	3	2	7	8	0.82	64 (3 m) 69 (17.5 m) 63 (40 m)
28 Aug 2009	14.7	—	—	0.53	6	9	4	2	7	9	0.99	72 (3 m) 55 (17.5 m) 40 (40 m)
25 Sep 2009	15.5	—	—	0.57	—	5	1	3	1	4	0.85	85 (3 m) 66 (20 m) 49 (50 m)
10 Nov 2009	9.6	—	—	0.68	—	—	4	7	2	9	—	—
1 Jul 2010	12.0	—	—	0.77	—	—	—	—	—	—	—	—
10 Sep 2010	10.7	—	—	—	—	—	—	—	—	—	—	—
22 Jun 2011	8.1	—	—	—	—	—	—	—	—	—	—	—
2 Sep 2011	11.9	—	—	—	—	—	—	—	—	—	—	—
RANGE	9.6–15.5	—	7–10	0.13–1.73	5–29	4–25	<1–8	<1–9	<1–35	2–53	<1–10	40–85
MEAN	12.8	—	8.4	0.57	9.9	7.2	2.4	3.4	5.0	8.4	1.40	60
SD	2.1	—	1.1	0.35	5.1	4.3	1.6	2.8	4.9	6.1	1.43	11.37

TABLE 2. Concentration ($\mu\text{g} \cdot \text{L}^{-1}$) of major cations measured from 3 sampling dates in 2009 at Fallen Leaf Lake, California.

	Al	Ba	Ca	Fe	K	Li	Mg	Mo	Na	Si	Sr	Notes
1 Jun 2009												
0 m	3.53	2.02	2740	4.20	406	0.29	287	<1.00	843	896	10.6	Little stratification
7.5 m	2.24	2.00	2640	<1.00	393	0.29	275	<1.00	852	857	10.0	
26 Jun 2009												
0 m	45.9	1.92	2412	2.01	409	0.34	260	<1.00	831	833	10.3	Epilimnion
12.5 m	8.90	1.92	2361	1.38	400	0.36	283	<1.00	857	893	10.6	Base epilimnion
25 m	12.7	2.00	2311	1.43	380	0.41	297	<1.00	889	885	10.8	Hypolimnion
27 Jul 2009												
3 m	36.7	1.97	2910	2.20	356	0.29	262	0.40	803	958	10.4	Epilimnion
17.5 m	45.4	2.05	2890	2.79	409	0.32	296	0.39	798	1030	10.8	Metalimnion
50 m	40.3	2.17	2980	1.76	441	0.38	324	0.36	820	1110	12.0	Hypolimnion

Spectrometry at the Nevada Bureau of Mines and Geology, University of Nevada (Table 2).

Lake trophic condition was quantified using a trophic state index (TSI) (Carlson 1977):

$$\text{TSI} = 14.42 \ln(\text{TP}) + 4.15,$$

where TP is the total phosphorus concentration ($\mu\text{g} \cdot \text{L}^{-1}$). Index values >50 indicate eutrophic conditions, and values >70 indicate hypereutrophic conditions (Wetzel 2001).

A 250-mL subsample of lake water from each depth was preserved by Lugol's addition. Diatom biomass was determined for water samples from 10 of the sample depths: 0, 3, 5, 10, 15, 17.5, 20, 25, 40, and 50 m for each of the 2009–2010 sampling periods. In 2011, the 3-m sample was eliminated and one at 30 m was added to better capture the vertical changes in diatom communities. The 250-mL water samples were settled and concentrated to 20 mL, and absolute abundance was determined by counting using a gridded 1-mL Sedgewick–Rafter counting cell at 400X magnification. A minimum of 5 rows of each counting cell (= 25% of 1-mL volume) were counted (mean $n = 682$). Cell counts were made at the genus level for both “live” (chlorophyll and lipids present) and dead cells (siliceous frustule only). Cell counts were converted to biovolume following Hillebrand (1999). Live cells of nondiatom algal groups were noted qualitatively but not counted, the most common being chrysophytes (*Dinobryon*, unspecified stomatocysts), dino-flagellates (*Ceratium* and *Gymnodinium*) and chlorophytes (*Botryococcus*, *Elakatothrix*). Small amounts of picoplankton (<6 μm) were also noted but were below the size limit for determination by our enumeration methods.

Permanent slide mounts were made in order to determine relative abundance counts ($n > 100$) for plankton tows and a subset of water depth samples (10, 20, and 50 m for 2009 samples). Permanent slides were made by drying a pipetted aliquot onto a coverslip and mounting the coverslip onto a glass slide using Zrax diatom mountant (boil mounts). These slides allowed for discrimination between live and dead material and were beneficial, along with the water samples, in differentiating between indigenous and washed-in taxa. Additional slides were made as burn mounts (USEPA 1973) and as strewn slides of siliceous slurries cleaned with hydrogen peroxide (Battarbee

1986) in order to aid in species-level identification. Diatoms were identified using a 1000X oil immersion lens with DIC on an Olympus BX51 microscope, and counts were made at 400X. Separate counts ($n = 100$) of the cyclotelloid fraction were made at 1000X. Photomicrographs and identification notes for common taxa may be found in the Appendix.

Data Analysis

Contour plots of diatom data were generated with the “filled.contour” function in R, version 2.15.0 (R Development Core Team 2012), using the interp algorithm in the package akima, version 0.5-7 (interpolation of irregularly spaced data; Akima et al. 2012). Annual precipitation data were extracted from PRISM (PRISM Climate Group 2012) for the latitude and longitude of Fallen Leaf Lake, and water-year total precipitation was calculated from 1 October of the previous year through 30 September of that year. Local annual snowfall data, collected from SNOTEL station 473 at Fallen Leaf Lake from 1980 to 2011, was accessed from the Natural Resources Conservation Services web site (NRCS 2012).

RESULTS

Field Measurements of Water Properties

Field measurements of water properties indicated a dilute system with a circumneutral pH and low alkalinity ($7.9\text{--}10\text{ mg} \cdot \text{L}^{-1}$), indicating a very limited buffering capacity (Table 1). Mean conductivity was low, averaging $21\text{ }\mu\text{S}$ (Fig. 2), and analysis of major cations showed concentrations in the range of a few hundred ppb for all but calcium (Table 2). In 2009, stratification had begun by 1 June, with the base of the epilimnion expanding from a depth of 12.5 m to a maximum depth of 17.5 m by late summer (Fig. 2). Dissolved oxygen profiles in 2009 showed an offset of $1\text{--}3\text{ mg} \cdot \text{L}^{-1}$ at 17.5 m, the base of the epilimnion, during the stratification months, and remixing to a minimum depth of 32 m in the fall (Fig. 2). Data collected in September 2010 from 40 m and 50 m showed a decrease in dissolved oxygen in the deeper hypolimnion ($>35\text{ m}$) but did not indicate anoxic conditions.

Interannual variations in stratification were also apparent in a comparison of the 3 years. The onset of stratification and the spring bloom was delayed in 2010 (Fig. 2) compared with

2009, owing largely to cooler spring temperatures and slower snowmelt. Although delayed, depth of stratification in 2010 eventually by the end of summer reached a depth similar to that in 2009 (17.5 m). In 2011, considerably higher winter precipitation and a deep snowpack combined with cooler spring temperatures resulted in delayed stratification and considerably shallower epilimnion development, which reached a depth of only 12.5 m by early September 2011.

Water clarity and chlorophyll *a* concentrations indicate the lake is presently oligotrophic, and nutrient concentrations are consistent with N-limitation (Table 1). The trophic state index calculated from surface TP measurements is 22–37, which suggests the lake is oligotrophic (Carlson and Simpson 1996). Secchi disk and chlorophyll *a* measurements also indicate oligotrophic conditions. From a nutrient standpoint, average monthly values of dissolved phosphorus (DP) and its bioavailable component, soluble reactive phosphorus (SRP), were low, never exceeding 13 ppb (Table 1). Highest values of DP were associated with the metalimnion during June and July (Fig. 3). Total phosphorus (TP) ranges from 5 to 29 ppb with a mean value of 9.9, indicating that the limited algal response measured by chlorophyll *a* concentrations may be a result of nitrogen limitation (Carlson 1983). Ratios of dissolved inorganic nitrogen (DIN) to dissolved phosphorus (DP) were <2 and supported nitrogen limitation (Table 1); however, nutrient bioassays conducted in 2006 indicated N limitation in the spring, changing to N–P co-limitation during summer and early fall (Chandra and Rost 2008). NO_3 levels were slightly elevated in the spring, likely owing to dissolved inorganic nitrogen entering the lake via spring runoff from higher in the watershed (Fig. 3). Highest NO_3 values in 2009, a fairly dry year, were recorded in June and did not exceed 10 ppb. In June 2011, an NO_3 measurement taken in Glen Alpine Creek entering Fallen Leaf Lake during a rapid period of snowmelt had a value of 21 ppb. NH_4 values were highest in late spring and summer 2009, with one high value of 35 ppb observed in surface waters on 26 June 2009 (Table 1, Fig. 3). This value may be spurious, or alternatively may represent high activity levels by excretors. Major ion analysis also shows low levels of micronutrients, including iron, molybdenum, and silica (Table 2). The July sampling

Fig. 2. Temperature, dissolved oxygen, and mean conductivity profiles at Fallen Leaf Lake, California. Note shallower epilimnion in 2011 (far left). Dates (mm-dd-yy) for the profile lines are given in the legends.

showed slight variation in silica between the epilimnion and upper hypolimnion, but overall values remained low, ≤ 1 ppm.

Seasonal and Vertical Distribution from Plankton Tows

Surface plankton tows from April to November 2009 indicated a seasonal diatom succession of *Aulacoseira subarctica* + *Nitzschia* spp. → *Asterionella formosa* + *Tabellaria flocculosa* strain IIIp → *Urosolenia eriensis* + *Fragilaria tenera*-group → *Handmannia bodanica*. *Aulacoseira subarctica* rapidly decreased in June, while araphids remained dominant throughout the spring bloom. *Urosolenia eriensis* and *F. tenera*-group had a significant peak in early June and then decreased substantially by early summer. Also present in the early spring tows were significant abundances of dead, washed-in taxa (Table 3), many of which were seen in boil mounts as dead specimens clumped with organic flotsam. Because the boil mounts preserved the chlorophyll inside the diatom frustules, it was possible to differentiate dead, washed-in taxa entrained in the water column from live taxa (Table 3). With the onset of stratification, *H. bodanica* became increasingly abundant and dominated the epilimnion in mid and late summer.

Vertical tows from 2009 provided a useful composite for comparison against the surface tows during the period of stratification (Fig. 4). Relative abundances varied markedly between surface and vertical tows, with *Aulacoseira subarctica*, *Asterionella formosa*, and *Tabellaria flocculosa* strain IIIp falling off dramatically in the surface yet remaining high in the composite. The tow from 25 September 2009 showed a marked vertical partitioning. For example, *Handmannia bodanica*, which dominated the surface tow, was grossly overshadowed by the abundance of *As. formosa* in the composite tow (Fig. 4). Vertical partitioning patterns were further elucidated through bio-volume counts of live taxa in discrete water samples and are discussed in detail below. Results from plankton tows taken in the spring and fall of 2010 and 2011 further support these general patterns of seasonal succession

Fig. 3. Contour plots of dissolved phosphorus and NO_3 concentrations (ppb) from discrete water samples taken in 2009 at Fallen Leaf Lake, California. Position of metalimnion is shown with 2 black lines.

TABLE 3. Diatom species observed in plankton tows and water samples from Fallen Leaf Lake, California. a = abundant, c = common, r = rare.

Diatom species	Live	Live, likely washed in	Dead, washed in
<i>Acanthidium</i> sp.			c
<i>Achnanthes peragalli</i>			c
<i>Asterionella formosa</i>	a		
<i>Aulacoseira humilis</i>	r	x	r
<i>Aulacoseira lacustris</i>			r
<i>Aulacoseira lirata</i>		x	r
<i>Aulacoseira perglabra</i>	r	x	r
<i>Aulacoseira pusilla</i>	r	x	r
<i>Aulacoseira subarctica</i>	a		
<i>Cocconeis placentula</i>			c
<i>Cyclotella antiqua</i>			r
<i>Cyclotella</i> cf. <i>ocellata</i>	a		
<i>Cyclotella glomerata</i>			r
<i>Cyclotella rossii</i>	a		
<i>Didymosphenia geminata</i>			r
<i>Discostella stelligera</i>			c
<i>Eumotia formica</i>		r	r
<i>Fragilaria tenera/nanana</i>	a		
<i>Fragilaria gracilis</i>	c		
<i>Fragilaria crotonensis</i>			r
<i>Fragilaria vaucheriae</i>			r
<i>Frustulia amphipleuroides</i>	r	x	r
<i>Handmannia bodanica</i>	a		
<i>Karayevia suchlandtii</i>			c
<i>Navicula aurora</i>			r
<i>Nitzschia acicularis</i>	r–c		c
<i>Nitzschia gracilis</i>	r–c		r
<i>Nitzschia frustulum</i>			r
<i>Nitzschia intermedia</i>	r		c
<i>Pinnularia</i> sp.	r	x	
<i>Stauroneis anceps</i>			r
<i>Stausira construens</i>	r	x	r
<i>v. venter</i>			
<i>Stausira pseudoconstruens</i>			r
<i>Stausirella martyi</i>			r
<i>Stausirella pinnata</i>	r	x	r
<i>Stephanodiscus medius</i>	r		
<i>Tabellaria fenestrata</i>	r	x	
<i>Tabellaria flocculosa</i> strain IIIp	a		
<i>Tabellaria flocculosa</i> strain IV	r	x	
<i>Urosolenia eriensis</i>	a		

and response to stratification, although there were interannual differences in species abundances.

A 30-m vertical composite taken in January 2012 provides a valuable winter snapshot, although the winter of 2011/12 was unusually dry, with November–December 2011 precipitation at roughly 6% of the 100-year average. There was a fair amount of organic flotsam in

the plankton tow, presumably remixed from the hypolimnion, and many diatom frustules were clumped within the flotsam. Of the live taxa, the most abundant were *Aulacoseira subarctica*, *Asterionella formosa*, *Nitzschia* spp., and *Cyclotella rossii*. Live *Tabellaria flocculosa* strain IIIp, *Handmannia bodanica*, and fragilarioid chains (e.g., *Stausirella pinnata*, *Stausira construens* var. *venter*, *Pseudostausira brevistriata*) were also present in subordinate amounts. *Fragilaria* frustules (*F. tenera*-group and *F. gracilis*) were common, but most appeared to be dead or degraded cells that were likely remixed from the hypolimnion. *Aulacoseira subarctica* was by far the most abundant *Aulacoseira* species; however, live and healthy-looking filaments of *Au. perglabra* and *Au. humilis* were also found. Based on the reported autecology of these low-mantled tycho planktonic species (Florin 1981, Camburn and Kingston 1986, Haworth 1988), it is likely that they were washed into the lake from marshy areas higher in the watershed and then resuspended when the lake was mixed in the late fall. Both *Au. perglabra* and *Au. humilis* are observed in small ponds and streams higher in the watershed. *Aulacoseira pusilla* and *Au. lirata* also occurred within the winter tow but most of these filaments appeared seriously degraded or dead.

Vertical Distribution from Discrete Depth Sampling

The chlorophyll maximum at Fallen Leaf Lake descends rapidly with the onset of stratification to form a seasonal deep chlorophyll maximum (DCM) in the hypolimnion that is roughly centered at 40 m (Fig. 5). Because diatoms dominate the algal populations in the spring, the chlorophyll maximum strongly correlates to the diatom maximum until late summer ($r = 0.86$ for June and July), when chrysophytes and dinoflagellates become an important component of the DCM. There was a marked compositional difference between the phytoplankton of the DCM and the epilimnion, similar to other deep transparent lakes, such as Lake Tahoe (Coon et al. 1987) and the Laurentian Great Lakes (e.g., Moll and Stoermer 1982). Floral compositions in these systems may vary from year to year in terms of which species are most dominant, but the compositional distinction between the DCM and epilimnetic floras remains (e.g., Barbiero

Fig. 4. Plankton tow data showing seasonal changes and variation in phytoplankton composition between the epilimnion (surface tow) and a composite water column (vertical tow) by late summer at Fallen Leaf Lake, California. Species shown are those with >1% abundance during the sampling (1 Jun 2009 and 25 Sep 2009).

Fig. 5. Chlorophyll *a* concentrations, phaeophytin corrected ($\mu\text{g} \cdot \text{L}^{-1}$), showing position of the chlorophyll maximum at Fallen Leaf Lake, California. Left: Contour plot of 2009 data. Position of metalimnion is shown by 2 black lines. The DCM at 40 m reached maximum intensity in August. Right: Vertical profiles of chlorophyll *a* from late season 2009 compared with early season data collected in 2010 showing downward migration of the DCM.

Fig. 6. Contour plots of live diatom biovolume ($1 \times 10^3 \mu\text{m}^3 \cdot \text{mL}^{-1}$ lake water) enumerated from discrete depths during 2009 at Fallen Leaf Lake, California. Position of metalimnion is shown with 2 black lines. November sampling occurred 3 days after a storm that mixed the lake down to 30 m. Panels: a, total biovolume; b, *Aulacoseira subarctica*; c, *Asterionella formosa*; d, *Tabellaria flocculosa* strain IIIp; e, *Fragilaria* spp.; f, cyclotelloids.

and Tuchman 2004). In Fallen Leaf Lake, several species found in abundance at the surface in early spring (*Aulacoseira subarctica*, *Asterionella formosa*, *Tabellaria flocculosa* strain IIIp) showed a “push down”; namely, peak abundances occurred at progressively deeper levels as seasonal stratification progressed (Fig. 6). Like the epilimnion, the DCM undergoes a seasonal succession, where *Au. subarctica*, a prominent DCM component in the early spring, was surpassed by *Asterionella* and *Tabellaria* in the later spring, and followed by *Cyclotella rossii*, plus chrysophytes and dinoflagellates in the late summer.

Several species peaked outside of the DCM, contributing to compositional differences between the DCM and epilimnion. *Urosolenia eriensis* and *Fragilaria tenera*-group, species found in high abundance in the surface only during the spring bloom, drop markedly in abundance in the summer. *Fragilaria* spp. (e.g., *F. gracilis*) remain a significant part of the epilimnion throughout the summer, and their maximum abundance is consistently found in the upper hypolimnion ~10–15 m above the DCM (Fig. 6). During the summer, the epilimnion is depleted in algal biomass and is dominated largely by *Handmannia bodanica* and *Dinobryon*. *Handmannia bodanica* appears to be well adapted to the warmer lower-density water of the epilimnion and seems unaffected by the high UV intensity. *Handmannia bodanica* did not have a specific peak abundance in the epilimnion, but the species composes a higher percentage of the epilimnion because of the reduction in other species. Overall, the effect on and control over the formation and intensity of the DCM are significant in Fallen Leaf Lake because the DCM is where the maximum production of diatoms occurs, and has a strong influence on the diatom biovolume exported to the sediment.

DISCUSSION

Deep Chlorophyll Maximum

There has been some discussion over factors controlling the formation and position of deep chlorophyll maxima, including UV inhibition effects, nutrient availability, and water density (Reynolds 1992, Saros et al. 2005, Camacho 2006, Harrison and Smith 2011). In high-elevation lakes, higher intensities, particularly of UVB radiation, have an effect on epilimnetic

phytoplankton composition (Harrison and Smith 2011). These higher intensities also may explain consistently low phytoplankton numbers in the upper 5 m of water, particularly in the early spring before the epilimnion was fully developed. *Handmannia bodanica* is well suited for the epilimnion because (1) it is a good N competitor and low-N specialist (Interlandi et al. 1999), (2) it can regulate its buoyancy, and (3) it has high light requirements (Saros et al. 2003).

The seasonal and vertical distributions of the major indigenous phytoplankton may be explained by known physiological requirements for these species. *Aulacoseira subarctica* shows highest abundances prestratification, descending to the upper hypolimnion and maintaining its peak abundance at greater depths (40–50 m) than other species (Fig. 6). A similar seasonal response of *Au. subarctica* has been observed in other temperate lakes and has been explained by its high sinking rate, low water temperature tolerance, low light requirements, and higher P requirements (Interlandi et al. 1999, Reynolds 2006). *Asterionella formosa*, like *Au. subarctica*, is also tolerant of wintery water temperatures but has considerably lower sinking rates than *Au. subarctica* (Reynolds 1984). Although an excellent P competitor (Interlandi et al. 1999), *As. formosa* is also highly responsive to nitrogen stimulation in N-limited alpine lakes (Saros et al. 2005), and its chronic high abundances in Fallen Leaf Lake may be driven by DIN. *Asterionella formosa* concentrations exceeded $40 \mu\text{m}^3 \cdot \text{L}^{-1}$ in the DCM in all 3 years during peak growth. Cyclotelloids, in general, are considered good N competitors, with good buoyancy regulation and low growth rates (Saros et al. 2003), all of which help explain the observed *Cyclotella rossii* growth peak in the DCM in late summer. The maximum intensity of the DCM was in late August, resulting from a combination of increased abundances of dinoflagellates and chrysophytes, residual standing crops of *Tabellaria flocculosa* strain IIIp, and increased growth of *C. rossii* to $>50 \mu\text{m}^3 \cdot \text{L}^{-1}$ (Fig. 6).

Nutrients and Phytoplankton Distribution

Distribution patterns of nutrients support the idea that the observed spring bloom intensity is in part governed by nutrient stimulation entering the lake during runoff. Dissolved inorganic nitrogen is expected to have the

Fig. 7. Precipitation, temperature, and historical transparency data for Fallen Leaf Lake, California, from 1969 to 2011: a, Transparency data plotted from values summarized in Reuter et al. (1996) for 1969–1994, Lico (2004) for 2002–2003, and this study for 2009–2011; b, Average spring temperature data show a 2.9 °C drop between 2009 and 2010–2011 spring temperatures showing lower spring temperatures for 2010 and 2011 relative to 2009; c, Precipitation data, where water year total precipitation is calculated from 1 October the preceding year through 30 September of that year, and where winter precipitation represents November through March totals. SWE = the cumulative snow water equivalent recorded at SNOTEL station 473 at Fallen Leaf Lake from 1980 to 2011. The 42-year winter precipitation average is shown with a horizontal line.

greatest stimulatory effect in N-limited systems, as indicated by numerous N-limited systems that have experienced recent stimulatory effects from dissolved inorganic nitrogen influxes (Saros et al. 2005). In particular, the presence of *Asterionella formosa* has been attributed to N deposition in other alpine lake systems, and indeed the Lake Tahoe Basin has experienced eutrophication, with atmospheric N deposition accounting for 55% of the total N

inputs (TERC 2011). Given that 80% of the precipitation in the Fallen Leaf Lake watershed originates as runoff from snowpack, it is expected that highest N concentrations should occur in the early spring during peak flow of Glen Alpine Creek. As mentioned previously, concentrations of N measured in 2009 were slightly elevated in the 1 June sampling (12 ppb maximum; Fig. 3) and may have potentially been higher earlier in the season, before our

sampling program had been established. The 2011 year experienced an unusually deep snowpack and low spring temperatures, and ice-out dates for several of the surrounding lakes were a full month behind the previous year (Fig. 7). Nutrient concentrations in Glen Alpine Creek, 0.5 km above Fallen Leaf Lake, were measured at 21 ppb during high discharge in late June 2011.

Interannual Variation

Over the 3-year monitoring period, there was a fair degree of variability in winter precipitation, spring temperature, and the strength and timing of stratification. The variability of these environmental attributes provides an interesting backdrop with which to consider the interannual variability in phytoplankton composition. To provide some perspective for evaluating the variability in the past 3 years of monitoring data, all previously published transparency, precipitation, and temperature data have been plotted back to water year 1970 (Fig. 7), when data was first collected for Fallen Leaf Lake by Goldman (Reuter et al. 1993). Both 2009 and 2010 showed average winter precipitation (Fig. 7), but the spring of 2010 was cooler than the preceding year, and stratification was delayed by about a month. As a result, the 1 July 2010 sampling shows a chlorophyll maximum at 12.5 m, which later descended to 40 m by the time of the second 2010 sampling in September. In contrast, 2011 was a heavy precipitation year, and a deep snowpack coupled with cool spring temperatures delayed spring runoff. In late June 2011, the upper parts of the watershed were still covered with snow, and there was considerable inflow from Glen Alpine Creek that persisted through July. In 2011, the DCM was shallower, centered at 30 m in early September. The shallower position of the DCM 2011 may best be explained by lower transparency, as Secchi depths were shallower in 2011 than in preceding years (Table 1, Fig. 7).

Diatom data from our 3 field seasons show variation in the dominant species, alternating between *Tabellaria flocculosa* strain IIIp (2009), *Asterionella formosa* (2010), and *Fragilaria tenera*-group (2011; Fig. 8). *Tabellaria flocculosa* strain IIIp distribution in the water column tracked seasonally with *As. formosa*, but its abundance was highly variable between seasons. *Tabellaria flocculosa* strain IIIp was

the most dominant diatom in 2009, and its peak abundance, centered in the DCM in midsummer, exceeded $150 \mu\text{m}^3 \cdot \text{L}^{-1}$. Though still present in 2010 and 2011, *T. flocculosa* strain IIIp was comparatively rare, peaking at $4 \mu\text{m}^3 \cdot \text{L}^{-1}$ in 2010 and $15 \mu\text{m}^3 \cdot \text{L}^{-1}$ in 2011. *Fragilaria tenera*-group also showed marked seasonal variation, dominating the epilimnion in the early spring bloom and then dropping off in the summer. In 2011, *F. tenera*-group was the dominant species, exceeding $95 \mu\text{m}^3 \cdot \text{L}^{-1}$ in the epilimnion in the spring, and its large numbers may have contributed to the lower transparency. Snapshots from the early 1990s also indicate interannual variation in the dominant phytoplankton species; however, there are insufficient data to discern long-term trends or patterns. In May 1991, planktonic *Tabellaria* identified as *T. fenestrata* (56%) and *Au. subarctica* (28%) were the dominant diatoms, and *As. formosa* and *F. tenera* group (identified as *Synedra radians*) were minor components (Reuter et al. 1993). In contrast, planktonic *Tabellaria* was a minor component in the 1994 spring bloom, which at its peak in May was dominated by *Cyclotella rossii*, identified as *C. kutzingiana* (>50%), followed by *F. tenera*-group (25%) and *As. formosa* (20%) (Reuter et al. 1996).

In the context of winter precipitation data, it is tempting to attribute increased *Fragilaria tenera* in 2011 to an increase in DIN load entering the lake. *Fragilaria tenera*-group shows a strong response in the early spring when NO_3 is highest. Unfortunately, there are no experimental data on the response of *F. tenera*-group to N stimulation, and this relationship is at best equivocal when the limited previous phytoplankton monitoring data are examined. There were slightly elevated abundances of *F. tenera*-group in 1994 relative to 1991 (Reuter et al. 1996), but both years were relatively dry (Fig. 7). In 1994, Lake Tahoe received 711 cm of precipitation, compared to 2057 cm in 2011. Calculated DIN loads for South Lake Tahoe for 1994 were $\sim 1200 \text{ g} \cdot \text{ha}^{-1}$, slightly lower than the 1991 loads (TERC 2011). It is possible that the rate of snowmelt and episodicity of nutrient pulses may be factors in species dominance through resource competition. Such was indicated by a culture experiment that simulated a P-limiting system with varied frequency of nutrient additions over a 35-d period (Suttle et al. 1987). All

Fig. 8. Interannual variability in diatom biovolume at Fallen Leaf Lake, California. *Tabellaria flocculosa* strain IIIp was the most dominant species in 2009, *Asterionella formosa* in 2010, and *Fragilaria tenera*-group in 2011. Cumulative biovolume represents the sum of biovolume ($\mu\text{m}^3 \cdot \text{mL}^{-1}$) from 10 depths counted from 0 to 50 m for each sampling period.

cultures received the same total amount of nutrients over the course of the experiment, yet those receiving additions every 4 and 8 days were dominated by a planktonic species identified as *Synedra radians*. Those with less frequent additions every 16 days were dominated by *T. fenestrata*. The potential relationship between species dominance and resource fluctuations for *T. flocculosa* strain IIIp versus *F. tenera*-group and/or *A. formosa* is intriguing and awaits testing in an N-limited system where nutrient influx is related to patterns of spring temperature snowmelt flux.

Cyclotelloid Distribution

A marked partitioning was observed between the 2 live species of cyclotelloids, namely *Cyclotella rossii* and *Handmannia bodanica*, both of which are common planktonic taxa in

oligotrophic lake systems. *Cyclotella rossii* was found in high abundances in the early spring, but was reduced in the epilimnion relative to *H. bodanica* during the stratification period. *Cyclotella rossii* numbers peaked in midsummer in the hypolimnion within the DCM. These spatial and seasonal variations are intriguing and may potentially be useful in discriminating stratification patterns in the fossil record. As a test, valve counts of the 2 cyclotelloid species were made from discrete water samples taken at depths of 0, 10, 20, and 50 m, as well as from the composite vertical plankton tows, from early June through September 2009 (Fig. 9). Composite counts made from the 70-m vertical plankton tows presumably show how the discrete partitioning is collapsed into the bottom sediment. There is a pronounced difference between early spring

Fig. 9. Relative percentage of valves of the 2 live cyclotelloid species, *Handmannia bodanica* and *Cyclotella rossii*, as counted from 4 water depths (0, 10, 20, and 50 m) and from 70-m vertical composite tows at Fallen Leaf Lake, California. In the spring (left), *C. rossii* represents roughly half of the epilimnetic valves and dominates the deeper samples. In the summer and early fall (right), *H. bodanica* dominates the epilimnion and upper hypolimnion. In both cases, the composite tows reflect each species' dominance.

(1 June and 26 June), when *H. bodanica* composed <20% of the valves in the composite tow, and mid to late summer, when *H. bodanica* accounted for >75% of the valves in the composite tow. Given the magnitude of the difference, it is logical to assume this ratio may be an effective proxy for the degree and duration of the stratification period, with higher percentages of *H. bodanica* relative to *C. rossii* representing years with stronger stratification.

The mixing depth, or depth of the epilimnion, has recently been linked to cyclotelloid species composition in P-limited oligotrophic lakes (Saros et al. 2012). *Handmannia bodanica* was shown to be dominant in lakes with greater mixing depths (14 m) than 2 other common cyclotelloid species inhabiting the suite of lakes studied, namely *Cyclotella comensis* and *D. stelligera* (Saros et al. 2012). *Cyclotella comensis* is part of the same species complex that includes *C. rossii*. Though our data show the potential for linking changes in the duration and depth of stratification with fossil cyclotelloid composition, the Saros et al. (2012) study indicates that long-term changes to lake thermal structure may also play a role in variations of cyclotelloid dominance, with stronger epilimnetic development favoring *H. bodanica*.

SUMMARY

Monitoring data from 2009 to 2012 show that the Fallen Leaf Lake phytoplankton

community is currently dominated by the araphid species *Asterionella formosa*, *Tabellaria flocculosa* strain IIIp, *Fragilaria tenera*-group, and *E. gracilis*, with lesser amounts of *Aulacoseira* (chiefly *Au. subarctica*), cyclotelloids (*Cyclotella rossii* and *Handmannia bodanica*), *Urosolenia eriensis*, and *Nitzschia*. There is a strong seasonal component that favors *Aulacoseira* and *Nitzschia* in the winter through early spring, shows short-lived peaks in *F. tenera*-group and *U. eriensis* in the spring bloom, and exhibits more persistent numbers of *As. formosa* and *T. flocculosa* strain IIIp through the spring and summer. Stratification results in a strong vertical partitioning of diatom species and the development of a deep chlorophyll maximum (DCM) that is centered in the hypolimnion between 30 and 40 m. The depth of the DCM appears to be related to light availability, as it was shallower in 2011 when Secchi depths were also shallower. Aside from winter production, the largest volume of diatom productivity is associated with the DCM. The DCM also shows a seasonal succession, with *C. rossii* becoming increasingly dominant in late summer and early fall. Strong vertical partitioning of cyclotelloid species is observed where *H. bodanica* increases from <20% to >75% of the valves in the composite water column. Ratios of *H. bodanica* to *C. rossii* may be a useful down-core proxy in gauging strength of past stratification.

Chronically high percentages of *Asterionella formosa* were documented for all 3 years, and

this species appears to be abundant year-round, moving into the meta- and hypolimnion during stratification. It will be important to examine its distribution down core to determine whether *As. formosa* abundance is a recent phenomenon in response to atmospheric N deposition, as has been proposed in other temperate N-limiting lake systems. Interannual variability was observed in the dominant diatom species. In all 3 years, the dominant species was an araphid but alternated between *Tabellaria flocculosa* strain IIIp, *As. formosa*, and *Fragilaria tenera*-group. Similarly, data from the early 1990s showed alternating dominance by araphid species and by *Cyclotella rossii* in one year. The years 2009–2011 varied widely in terms of winter precipitation, spring temperature, runoff and nutrient influx, and onset and strength of stratification. Unfortunately, there are insufficient data and too many variables to presently tie the variation in dominant species to any of these factors. Future long-term monitoring, as well as experimental work on resource requirements and nutrient response of *T. flocculosa* strain IIIp and *F. tenera*-group, will be needed to determine the principal causes of interannual variation in the dominant araphid species. Finally, a significant component of the valves found in winter and early-spring water samples are washed-in littoral, stream, and marsh species from higher in the watershed. There are negligible areas of periphyton growth in the lake today, and identification of the washed-in components will be useful in down-core reconstructions.

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APPENDIX (FIGURE ON FACING PAGE).—Diatom photomicrographs and taxonomic notes. Transmitted light and scanning electron photomicrographs were taken of diatoms from water samples and surface sediment from Fallen Leaf Lake, Sierra Nevada, California. Transmitted light photos taken with plane-polarized light are specified as “nonDIC” and those taken with a differential interference contrast filter are specified as “DIC.” Scanning electron images taken with an Hitachi-SM1000 tabletop SEM are specified as “SEM-ENV,” and those taken with a JEOL JSM-6700-F field emission SEM are specified as “SEM-FE.”

1. *Aulacoseira subarctica* (Müller) Haworth 1988.

a, DIC surface sediment, scale = 10 μm ; b, SEM-FE surface sediment, scale = 10 μm .

Taxonomic notes: Specimens commonly with a diameter of 7 μm , long mantle height, valve face imperforate, 1 spine per 2 rows of costae.

2. *Aulacoseira lirata* (Ehrenberg) Ross in Hartley 1986.

DIC surface sediment, scale = 10 μm .

Taxonomic notes: Diameter commonly >10 μm , collum is prominent, coarse round areolae in straight rows, 1 spine per row of costae, imperforate flat valve face, deep ringleiste.

3. *Aulacoseira perglabra* (Østrup) Haworth 1988.

a, DIC surface sediment, scale = 10 μm ; b, SEM-ENV surface sediment, top view is into valve interior, scale = 5 μm .

Taxonomic notes: Diameter commonly 6–8 μm , low mantled, mantle areolae are rare and sporadic in transmitted light, 1 row at peripheral margin below spine insinuation is variably developed, long linking spines, no ringleiste, valve face imperforate, concave.

4. *Aulacoseira pusilla* (Meister) Tuji & Houki 2004.

a, DIC surface sediment, scale = 10 μm ; b, nonDIC of valve face from surface sediment, scale = 5 μm ; c, SEM-FE surface sediment showing external view of ringleiste, linking spines also visible, scale = 5 μm ; d, SEM-FE surface sediment showing internal view of ringleiste, rimoportulae are marked with arrows, scale = 5 μm ; e, SEM-ENV showing perforate valve face and linking spines, scale = 5 μm .

Taxonomic notes: Diameter ≥ 7 μm , valve-to-mantle ratio of 1:1 or less. Valve face is flat and ranges from densely perforate to sparse and irregularly punctate. Linking spines same structure as *Au. subarctica*, except commonly shorter and blunter, ringleiste deep, 4–6 rimoportulae on ringleiste are observable in valve view.

5. *Aulacoseira humilis* (Cleve-Euler) Genkal & Trifanova in Trifanova & Genkal 2001.

a, DIC surface sediment, scale = 10 μm ; b, SEM-ENV surface sediment, scale = 1 μm .

Taxonomic notes: Small diameter, commonly 5 μm , small double rows of mantle areolae set in

straight grooves gives striped appearance in mantle view, mantle costae prominent, 1 long and thin linking spine per costa, valve face coarsely punctate.

6. *Fragilaria nanana* Lange-Bertalot 1991, included in *Fragilaria tenera*-group.

Valve view, nonDIC from cleaned surface water sample, scale bar = 10 μm .

Taxonomic notes: Long and thin, 40–90 μm , 1.5–2 μm diameter, apices slightly capitate, striae straight and appear to alternate, varying from 19–24 μm (commonly 22–23 μm) in live specimens, which fits *F. nanana* striae counts (21–24/10 μm). *Fragilaria tenera* (W. Smith) Lange-Bertalot 1980 has fewer striae (17–20/10 μm). Shorter specimens (30–35 μm length), encountered in water samples, that did not taper as much apically and were 2 μm wide were assigned to *F. gracilis* Østrup 1910. All 3 species were enumerated within the *F. tenera* group in water samples because they are difficult to discriminate at 400X in a Sedgewick–Rafter counting cell.

7. *Urosolenia eriensis* (H.L. Smith) Round & Crawford in Round, Crawford, and Mann 1980.

DIC from water spring surface sample, scale bar = 10 μm .

8. *Nitzschia* sp.

Live specimen from winter surface water sample, nonDIC, scale bar = 10 μm .

9. *Tabellaria flocculosa* strain IIIp sensu Koppen 1975.

SEM-FE from a spring water sample.

Taxonomic notes: Commonly 50–60 μm long, slight torsion in valves, apices capitate and may appear asymmetrical. Fine marginal spines observable in SEM and transmitted light, median inflation only slightly wider than apices, copulae complete and with a rudimentary septum.

10. *Asterionella formosa* Hassall 1850.

Live colony from spring water sample, nonDIC, always forms stellate colonies, scale bar = 20 μm .

11. *Tabellaria flocculosa* strain IIIp sensu Koppen 1975.

Live material from spring water sample, nonDIC, forms colonies, scale bar = 20 μm .

12. *Fragilaria tenera* group and *T. flocculosa* strain IIIp.

Stellate colony typical in *F. tenera* group (likely *F. nanana*), scale bar = 10 μm .

13. *Handmannia bodanica* (Eulenstein ex Grunow) Kociolek & Khursevich in Khursevich and Kociolek 2012.

a, Cleaned specimen from surface water sample, DIC, scale bar = 10 μm ; b, SEM-FE from surface sediment, scale bar = 10 μm ; c, SEM-FE from water sample, view of inner valve face showing *Schattenlinie* at margin, 2 rimoportulae, and distribution of cribrate areolae and fuloportulae, scale

bar = 10 μm ; **d**, SEM-FE from surface sediment openings of rimoportulae indicated with arrows, scale bar = 10 μm .

Taxonomic notes: Valve 18–25 μm diameter, face with slight concentric undulation. Valve center with numerous areolae and fuloportulae, annulus absent, valve margin striate, some forked striae branch at margin, with 2 rimoportulae. In SEM, 2 rimoportulae appear as enlarged pores in marginal area of valve face, both with labiate processes on inner valve face. Central fuloportulae with 3 satellite pores, and areolae with internal cribra. In terms of varieties, none is specified at this time. The pattern of striae and areolae, and the disposition of mantle rimoportulae and fuloportulae vary from the nominate variety, as well as from *v. affinis* and *v. intermedia*.

14. *Cyclotella rossii* Håkansson 1990.

a and **b**, external views of valve SEM-FE from surface sediment, note differences in ornamentation of central area, scale bar = 5 μm ; **c**, and **d**, SEM-FE from surface sediment, internal views of valve faces showing *Schattenlinie* at margin,

rimoportulae, and several fuloportulae at center, scale bar = 5 μm .

Taxonomic notes: Valve diameter 8–20 μm , valve face fairly flat, central area highly variable with ornamentation of variable size and arrangement, may be ocellate, with 3–4 ocellae. Several fuloportulae in central area, and 1 rimoportula present in center of marginal area, rimoportulae seen on inner valve face, and central fuloportulae with 2 satellite pores. It is unclear whether this is one highly variable species or multiple species within a species group.

15. *Discostella stelligera* (Cleve & Grunow) Houk & Klee 2004.

a, DIC from cleaned water sample, scale bar = 1 μm ; **b**, SEM-FE external stellate valve face from surface sediment, scale bar = 1 μm ; **c**, SEM-FE internal view of stellate valve face from surface sediment, scale bar = 1 μm ; **d**, SEM-FE internal view of nonstellate valve face from surface sediment.

Taxonomic notes: Valves small, usually <10 μm , may be polymorphic with one stellate and one nonstellate valve.