

A Case History: Effects of Mixing Regime on Nutrient Dynamics and Community Structure in Third Sister Lake, Michigan During Late Winter and Early Spring 2003

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Abstract

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We studied the winter to spring transition in Third Sister Lake (TSL), a small glacial lake in southeastern Michigan, to determine the effect of mixing regime on nutrient dynamics and community structure in an urban temperate lake. After ice-off, the oxycline was mixed downward from 3 to 6 m depth, resulting in addition of 5 mg m⁻² P-SRP, 857 mg m⁻² N-NH₄⁺, and 400 mg m⁻² N-NO₃⁻ to the epilimnion, but trapping 299 mg m⁻² P-SRP, 7877 mg m⁻² N-NH₄⁺ and 36 mg m⁻² N-NO₃⁻ in the bottom waters. Nutrients supplied by snow melt runoff (138 mg m⁻² P-SRP, 430 mg m⁻² N-NH₄⁺, 596 mg m⁻² N-NO₃⁻) were an order of magnitude greater than rain event loads (0.13 mg m⁻² P-SRP, 0.17 mg m⁻² N-NH₄⁺, and 1.05 mg m⁻² N-NO₃⁻) during the transition time from ice cover to open water. Reduced spring mixing did not have a large impact on N:P molar ratios, because external N:P ratios were low (7.5) compensating for reduced supply of P from the bottom waters. Bacterial production was greater in the hypolimnion than in the epilimnion, and mesocosm experiments showed that bacteria were P limited in the epilimnion but not in the hypolimnion. Total algal and zooplankton densities increased after ice-out, while *Daphnia* and *Bosmina* densities decreased. Increases in zooplankton grazing rates after ice-off were most dramatic in small-bodied zooplankton. Sediment core analysis showed that *Asterionella* relative abundance continues to increase, suggesting that the lake has become more brackish and oligotrophic. Our findings suggest that TSL has undergone a transition from dimictic to meromictic conditions, and that continued salt inputs have altered the structure and function of this ecosystem.

Key Words: meromixis, nutrient dynamics, N:P ratios, productivity, road salt inputs, sediment core, snow melt, spring turnover

Spring and fall turnover events are important drivers of overall biogeochemistry of temperate-zone lakes. Complete mixing oxygenates the bottom waters and redistributes nutrients that accumulate during stratified periods from bacterial mineralization in the sediments. The extent and timing of spring mixing depends on climate, lake morphology, wind speed and direction, degree of shelter from wind, and presence and strength of a pycnocline in the water column. This latter factor is influenced by anthropogenic road salt inputs. Numerous studies have documented increases in chloride (Cl⁻) concentrations in streams (Shanley 1994, Lofgren 2001, Godwin *et al.* 2003) and lakes (Judd 1970, Driscoll *et*

al. 1991, Rosenberry *et al.* 1999). The effects of road salts include reduced nutrient availability to plants and increased cation and heavy metal leaching through cation exchange in soils (Mason *et al.* 1999, Backstrom *et al.* 2003). In some lakes, salt inputs have altered mixing regimes by reducing spring mixing and prolonging summer stratification (Bubeck *et al.* 1971).

Third Sister Lake (TSL) is a small moderately eutrophic temperate lake that has experienced rising water conductivity and salinity over the last two decades due to the use of deicing salts in the catchment (Hammer 1995, Bridgeman *et al.* 2000). Past studies indicated that the lake regularly turned over in

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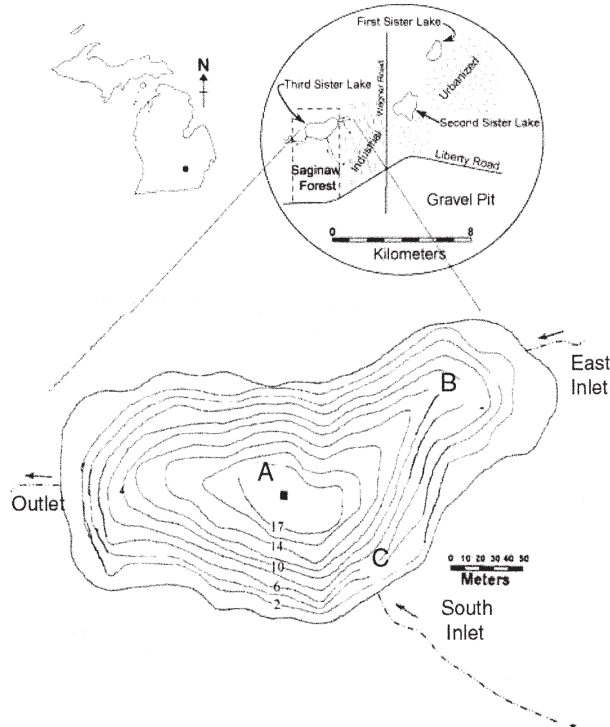


Figure 1.-Bathymetric map of Third Sister Lake. Samples were taken at sites A, B, and C.

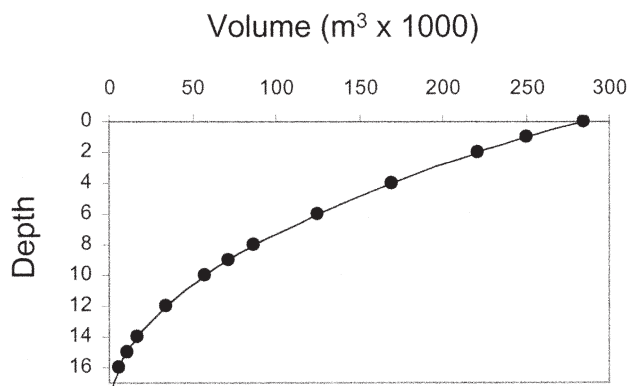


Figure 2.-Hypsographic curve for Third Sister Lake.

spring and fall (Eggleton 1931), but recent surveys suggest that complete mixing in TSL now occurs only infrequently (Bridgman *et al.* 2000).

Changes in the spring mixing regime may have strong effects on nutrient dynamics. In temperate lakes that turnover, spring phytoplankton blooms are fueled by nutrients generated in bottom waters over the winter. Incomplete mixing after ice-off prevents the redistribution of bottom water nutrients to the trophogenic zone, where they could fuel primary production. Nutrient availability in the spring may also control bacterial activity (*e.g.*, Vadstein 2000). TSL bacterioplankton

are P limited during the spring and fall turnovers (Cotner and Wetzel 1992) and may out-compete phytoplankton for nutrients at this time. Failure of a lake to turnover, therefore, can impact spring plankton dynamics, and decreased mixing over the course of several years will alter the energy flow and trophic status of a lake.

Changes in nutrient dynamics and redox potential may also impact community composition of phytoplankton (Hammer and Stoermer 1997), zooplankton, and benthic invertebrates (Eggleton 1931, Doke *et al.* 1995). There is evidence that shifts in the relative abundance of diatoms in the sediments (Hammer and Stoermer 1997) and the diversity and abundance of benthic invertebrates (Bridgeman *et al.* 2000) are related to shifts in spring and fall mixing dynamics. Trophic cascades or low O₂ conditions may affect zooplankton communities and higher trophic levels. These changes in community structure may alter how the lake responds to nutrient pulses and other disturbances.

To better understand the physical, chemical, and biological changes associated with anthropogenically induced meromixis, we studied TSL over the winter to spring transitional dynamics, (2) determine the extent of mixing that occurs in the weeks following ice off, and (3) develop nutrient budgets to determine how reduced mixing affects the relative importance of internal versus external nutrient loading and the resulting changes in ecosystem function (primary and bacterial productivity) and structure (phytoplankton and zooplankton community composition). We used field data to construct budgets of chloride and nutrients, and laboratory experiments to further investigate how physical and chemical changes due to meromixis would impact the biological system.

Methods

Site Description

Third Sister Lake (42°17'N, 83°48'W) is located in southeast Michigan, three miles west of Ann Arbor (Fig. 1). It is a small kettle lake (3.85 ha) that is relatively deep ($z_{max} = 17.5$ m $z_{mean} = 8$ m; Fig. 2), moderately eutrophic, with 5 to 40 μ g Chl *a*/L (Lehman and Naumoski 1986), and a catchment area of 110 ha. The lake has two intermittent inflows, a small creek to the east (East Inlet) and a stream entering from the south (South Inlet; 85% of total inflow). The South Inlet drains a catchment which includes forested and developed lands and two major roads. The East Inlet drains a smaller sub-catchment which includes parking lots of an industrial complex that was built 500 m to the east of the lake in the late 1970s. An intermittent outflow to the west drains into the Huron River. The lake is surrounded by 13.2 hectares of trees that were planted between 1904-1937 (Hammer 1995).

The main sampling station (Site A, $z \sim 17.5$ m; Fig. 1) was located in the center of the lake at its maximum depth. Site B was located near the South Inlet ($z \sim 2$ m), and site C was located in the western portion of the lake ($z \sim 7.5$ m).

Sampling

We sampled on five dates in 2003: twice under ice (28 February, 13 March), the day of ice-off (27 March), and twice after ice-off (1 and 8 April). Oxygen and temperature profiles were measured at 1 m depth intervals (YSI 55). Water was collected with a Van Dorn bottle at 2, 6, 9 and 15 m. Conductivity (Orion Model 128) and pH were measured at each depth, and water was stored in dark bottles on ice for transport to the lab. On the latter three dates, temperature, conductivity, and fluorescence measures were taken using a Seabird Conductivity- Temperature- Depth (CTD) meter with attached Self Contained Underwater Fluorescence Apparatus (SCUFA). Plankton tows were taken to 13 meters using 64 μm (phytoplankton) and 200 μm (zooplankton) mesh nets. Phytoplankton and zooplankton samples were stored in Lugol's solution and formalin, respectively. Samples were concentrated and counted following quantitative procedures of Wetzel and Likens (1991). We collected samples for Chlorophyll *a* (Chl *a*) determination (acetone extractions, Wetzel and Likens 1991) at three depths on 28 Feb, and at the surface only on the remaining sample dates. At sites B and C, we collected only surface water samples. We sampled the inlet waters during snow melt (15-17 March, South Inlet only) and a large rain event (4 April; both South and East Inlets). We calculated stream discharge using stream velocity (G.O. Environmental Flow Meter) and cross-sectional area measurements.

Samples for chemical analysis were filtered (Whatman GF/C filter) within two hours of collection and analyzed within two days (snow melt and rain event samples were frozen and analyzed within 2 hours of melting). Soluble reactive phosphorus (SRP) was measured colorimetrically using a molybdate method (Strickland and Parsons 1972). Ammonium (NH_4^+) concentrations were measured using the phenate method (Solorzano 1969). Nitrate (NO_3^-) concentrations were measured spectrophotometrically using a cadmium reduction to nitrite on an Alpkem autoanalyzer. Dissolved organic carbon (DOC) samples were acidified to pH ~ 3 and stored at 4°C in the dark until analysis using a high-temperature platinum-catalyzed combustion followed by infrared detection of CO_2 (Shimadzu TOC-5000). Samples for cations (Ca^{2+} , Mg^{2+} , Na^+ , K^+ ; note, no samples collected on 1 April 2003) were acidified (100 μL 6 N HCl in 60 mL sample) and analyzed on a Perkin Elmer 3300 inductively-coupled plasma optical emission spectrophotometer, and major anions (Cl^- and SO_4^{2-}) were analyzed on a Dionex ion chromatograph. All water samples were charge-balanced to within 5% of total ionic charge.

Calculations

We calculated inflow water density using temperature and partial molar volume contributions of dissolved salts (Kling *et al.* 1989). Nutrient budgets were calculated using bathymetric (Fig. 1, Eggleton 1931) and nutrient concentration data. Loadings of Cl^- and nutrients were calculated by integrating discharge and concentrations over snow melt and rain event sampling periods. Based on density calculations, we allocated nutrient inputs to either the epi- or hypolimnion (defined as the zones above and below the oxycline). Nitrogen to P ratios (N:P) were calculated based on SRP to total dissolved N. *In situ* fluorescence was converted to Chl *a* by regressing Chl *a* and SCUFA readings for depths at which we had both Chl *a* and fluorescence ($n = 9$, $R^2 = 0.96$). We estimated the potential phytoplankton biomass that nutrient loads could support using Redfield ratios (Stumm and Morgan 1981). Standing stocks of phytoplankton biomass were estimated by integrating Chl *a* over depth and converting Chl *a* to C (Harris 1986).

Bacterial Bioassays

Bacterial production (BP) was measured at 2 and 9 m (to characterize the epi- and hypolimnion respectively) using the ^{14}C - leucine incorporation method (Simon and Azam 1989). Because reduced mixing impacts both nutrient availability and water column temperature during the winter to spring transition, we conducted mesocosm experiments in which both factors were manipulated (1 μM SRP addition and two temperatures: 4 and 13°C). On 1 April, water from 2 and 9 m was filtered through 3 μm pore size filters to exclude most algae (confirmed by microscopy). Mesocosms (500 mL) of filtered water were incubated in the dark, and BP was measured at 0, 2 and 5 days. DOC and SRP were measured at the start and termination of the experiment.

Phytoplankton and Zooplankton

Phytoplankton and zooplankton communities were described before and after ice-off by counting and identification to genera ($N = 3$ for each date). To understand interactions between primary and secondary production over the winter-spring transition, we measured the grazing rates of small- and large-bodied zooplankton before and after ice-off. BOD bottles were filled with filtered (50 μm) lake water from 1 m. Treatments (in triplicate) included the addition of large-bodied or small-bodied zooplankton. A 500 μm mesh sieve was used to separate the two groups, and control bottles received no zooplankton. Three initial bottles were immediately filtered to remove phytoplankton for Chl *a* analysis. The remaining bottles were incubated for 1.5 hours (13 March) or 3 hours (1 April) at 4°C in the dark. Treatment bottles were filtered (50 μm) to remove zooplankton. Zooplankton biomass was oven dried (40°C) and weighed. Each bottle was then filtered

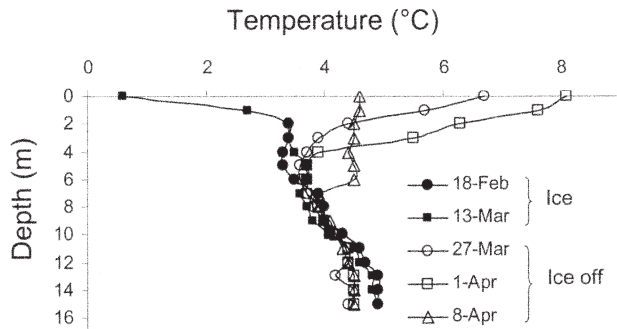


Figure 3.-Temperature at site A on sampling dates under ice (18 Feb and 13 March) and after ice-off (27 March, 1 April, and 8 April 2003).

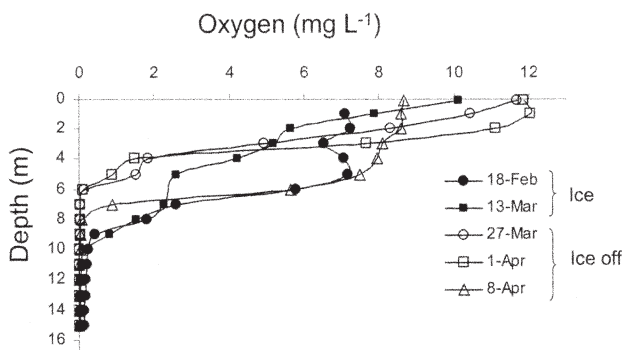


Figure 4.-Oxygen concentration at site A on sampling dates under ice (18 Feb and 13 March) and after ice-off (27 March, 1 April, and 8 April 2003).

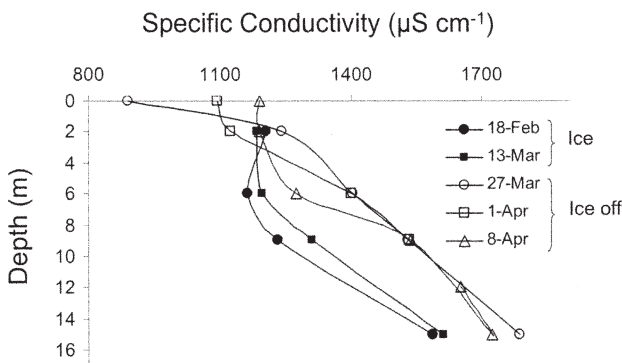


Figure 5.-Specific conductivity throughout the water column at site A on sampling dates under ice (18 Feb and 13 March) and after ice-off (27 March, 1 April, and 8 April 2003).

for Chl *a* analysis. Consumption rates were calculated as the difference between initial and treatment Chl *a* levels over time per unit of zooplankton biomass.

Cores

To document recent changes in diatom community composition (see Hammer and Stoermer 1997 for information prior to 1994), two sediment cores were removed from the central basin ($z = 17.5$ m) with a gravity corer. Cores were sealed and transported to the lab and stored at 4°C. Dark and light bands were assigned odd and even numbers respectively. Cores were bisected horizontally, carefully cleaned with a scalpel, and photographed. Sub-samples of 250 mg wet weight were removed from specific bands in the top, middle, and bottom portions of Core A. Two organic (8 and 17 cm core depth) and clay (2 and 17.5 cm) samples were removed from Core A. An Ekman dredge supplied the fifth sample of surface sediments. Slides were prepared following the procedure of Battarbee (1973). Diatom counts were calculated using relative abundances, and major taxa were identified to genus. Cores were not dated in this study.

Results

Temperature / Oxygen / Conductivity

Temperature profiles under ice showed typical inverse stratification; however, bottom waters exceeded 4°C (Fig. 3). After ice-off (27 March), solar radiation increased surface water temperatures, and by 8 April, a thermocline had established at 6 m. The anoxic zone increased in thickness throughout the winter (Fig. 4); the depth at which O_2 concentrations was less than 1 mg/L rose from 9 m (18 Feb, 13 March) to 6 m (27 March). The oxycline rose until ice-off from 6.5 m (18 Feb) to 5 m (13 March) to 3 m (27 March). On 27 March, 60% of the lake had O_2 levels < 2 mg O_2 /L. After ice-off, O_2 levels increased in surface waters and the oxycline dropped to 6 m by 8 April. Below 6 m, O_2 levels continued to decrease. Specific conductivity increased with depth (Fig. 5). After ice-off, specific conductivity decreased in the epilimnion, and was especially low at the surface on 27 March.

Specific conductivity of inflow water decreased with increasing discharge (Table 1). Conductivity, cations, and anions were higher at the East Inlet than the South Inlet. Conductivity of snow melt runoff was initially lower than lake surface water, but increased surpassing conductivity of lake water as discharge declined (Table 1). In the East Inlet, nutrients, cation, and anion concentrations were greater and conductivity was 2-3 times higher compared to the South Inlet. However, the calculated density of the East Inlet discharge was still low enough to allow the inflow water to spread out over the surface of the lake (Table 1).

Table 1. Discharge (Dischg), specific conductivity (Sp Cond: at 25°C) density, and concentration of nutrients, cations, and anions at sample times of snow melt and rain events (2003). The depth at which inflow water was injected for each sample time is indicated in the column labeled "z." Total inputs were calculated by integrating between time points of measurement.

	Time	Stream Dischg. L/sec	Sp Cond µS/cm	Density g cm ³	Z m	SRP µg P/L	NH ₄ ⁺ µg N/L	NO ₃ ⁻ µg N/L	Cl ⁻ mg/L	SO ₄ ²⁻ mg/L	Ca ²⁺ mg/L	Mg ²⁺ mg/L	Na ⁺ mg/L	K ⁺ mg/L	Fe ³⁺ mg/L	Mn ²⁺ mg/L	
Snow melt																	
<i>S. Inflow</i>																	
	15 March	14:10	103.4	570	0.999976	< 2	210.5	556.3	1071.8	135.8	17.46	17.41	2.97	90.2	12.50	0.00	0.01
	15 March	18:30	65.6	370	0.999979	< 2	220.4	665.6	1095.6	77.0	12.52	13.87	3.39	53.8	10.99	0.00	0.02
	16 March	12:30	413.8	411	1.000076	>16	157.9	491.2	636.1	93.3	10.90	11.21	3.49	58.8	10.70	0.00	0.03
	17 March	7:45	3.3	1745	0.999293	< 2	123.7	447.7	473.5	468.7	33.04	35.85	6.96	287.7	20.30	0.00	0.12
	Total (kg)					5.3	16.7	23.1	4726	472	499	126	2979	391	0	1	
Rain event																	
<i>S. Inflow</i>																	
	4 April	8:30	17.6	516	1.000020	2-6	83.6	108.9	528.1	122.9	19.62	13.78	1.93	90.0	4.07	0.00	0.00
	4 April	12:45	38.34	608	1.000015	2-6	72.0	65.2	353.0	142.9	20.05	15.60	2.17	106.1	4.37	0.00	0.01
	4 April	15:00	14.14	843	1.000025	2-6	51.4	46.3	379.8	207.1	26.66	22.61	3.34	139.2	6.00	0.00	0.00
	Total (kg)					0.05	0.05	0.29	101	23	16	2	108	5	0	0	
<i>E. Inflow</i>																	
	4 April	8:30	5.94	1424	0.999961	< 2	56.0	67.9	359.8	386.2	49.48	23.32	3.14	253.0	4.45	0.00	0.02
	4 April	12:45	4.305	1358	0.999978	2	28.3	42.4	296.8	366.7	47.77	26.26	3.01	233.7	4.14	0.00	0.02
	4 April	15:00	2.25	1500	0.996968	< 2	22.4	28.0	301.9	403.5	48.13	30.95	3.89	246.2	4.21	0.00	0.02
	Total (kg)					0.01	0.01	0.04	47	6	3	0	30	1	0	0	

Table 2.-Depth profiles of physical and chemical measures in TSL over the 2003 winter-spring transition.

Date	Depth m	Sp. Cond. µS/cm	Density g cm ³	SRP µg P/L	NH ₄ ⁺ µg N/L	NO ₃ ⁻ µg N/L	Cl ⁻ mg/L	SO ₄ ²⁻ mg/L	Ca ²⁺ mg/L	Mg ²⁺ mg/L	Ba ²⁺ µg/L	Na ⁺ mg/L	K ⁺ mg/L	Mn ²⁺ mg/L	Fe ³⁺ mg/L	DOC µM
18 Feb	2	1205	1.000040	34.6	337.9	131.7	293.0	9.2	44.3	8.5	36.5	177.9	7.8	0.1	0.0	
	6	1165	1.000037	31.5	547.7	134.2	303.8	8.9	43.9	8.4	40.3	176.7	7.4	0.1	0.0	
	9	1232	1.000044	28.9	1951.5	71.9	309.6	8.7	44.1	8.4	54.1	186.7	7.6	2.5	0.0	
	15	1588	1.000062	492.0	10998.3	31.4	445.7	2.4	43.3	8.2	31.1	174.5	7.4	0.3	0.0	
13 March	0.01	-	0.996968	-	-	-	287.1	9.9	42.4	8.1	81.8	172.2	8.3	0.0	0.0	
	2	1184	1.000036	13.3	467.2	179.6	296.7	11.5	47.1	9.3	54.9	189.3	8.5	0.0	0.0	946.8
	6	1196	1.000037	26.2	900.3	152.9	301.6	9.0	43.7	8.3	26.2	178.3	7.6	0.7	0.0	
	9	1312	1.000048	0.0	1471.9	152.0	337.0	9.2	44.9	8.3	61.7	199.9	8.0	2.9	0.0	621.0
27 March	15	1612	1.000062	382.7	13435.0	0.0	408.6	2.5	51.0	9.2	1428.6	238.2	9.3	4.7	8.2	
	0.01	-	0.996968	-	-	-	217.0	9.3	33.7	6.4	71.7	137.8	6.9	0.0	0.0	
	2	1241	1.000032	1.7	155.6	221.3	288.0	9.1	45.5	8.5	63.2	183.6	7.9	0.0	0.0	547.8
	6	1404	1.000044	0.7	1296.1	218.2	337.9	10.1	45.9	8.4	69.7	210.1	8.7	1.7	0.0	
1 April	9	1531	1.000056	3.1	3544.6	37.7	374.9	8.1	46.5	8.4	96.2	226.3	8.6	3.6	0.5	563.1
	15	1786	1.000071	258.9	9144.5	2.2	424.5	5.9	49.5	9.0	72.7	256.3	9.6	3.9	2.3	
	2	1080	-	0.1	1.5	-	-	-	-	-	-	-	-	-	-	515.9
	6	1350	-	0.0	43.1	-	-	-	-	-	-	-	-	-	-	547.2
8 April	9	1490	-	0.2	109.8	-	-	-	-	-	-	-	-	-	-	-
	15	1650	-	9.6	274.3	-	-	-	-	-	-	-	-	-	-	-
	2	1124	0.999978	1.6	47.3	199.7	283.9	10.0	41.6	7.8	69.5	175.4	7.8	0.3	0.0	541.6
	6	1401	1.000045	0.0	1378.4	170.7	304.5	10.3	42.2	7.9	72.9	182.6	7.9	0.8	0.0	
15 April	9	1533	1.000057	6.6	3513.5	3.7	373.2	7.5	46.0	8.5	97.3	221.2	8.3	4.0	1.2	524.3
	15	-	1.000067	305.9	8776.5	3.5	419.6	4.6	50.0	9.0	108.1	255.5	9.4	3.9	4.5	

Table 3.—Nutrient budget for TSL epilimnion based on the snow melt event (water injected < 6 m), a 4 April rain event (S. and East Inlets), and nutrient supply from bottom waters under two scenarios: mixing to 6 m and complete mixing. For comparison, standing stocks of Chl a and C-phytoplankton are shown for two dates.

	P into epi. (kg)	NH ₄ ⁺ into epi. (kg)	NO ₃ ⁻ into epi. (kg)	N:P	C in epi phytop. (kg)	C in epi phyto (g m ⁻²)	Chl a in epi. (g)
Snow melt event	3.8	12.02	16.74	7.5	190.5	0.98	3810
Rain event	0.056	0.061	0.342	7.2	2.7	0.01	53
Mixing to 6 m	0.225	33.25	15.45	216	23.8	0.12	476
Complete mixing	6.664	190.02	9.46	30.0	706.4	2.15	14128
Total (6 m mixing)	4.09	45.33	32.53	18.9	217.0	1.63	8741
Total (complete mixing)	10.56	202.27	26.54	21.7	899.6	3.26	22393
1 April standing stock					91.4	0.47	1829
8 April standing stock					67.1	0.35	1353

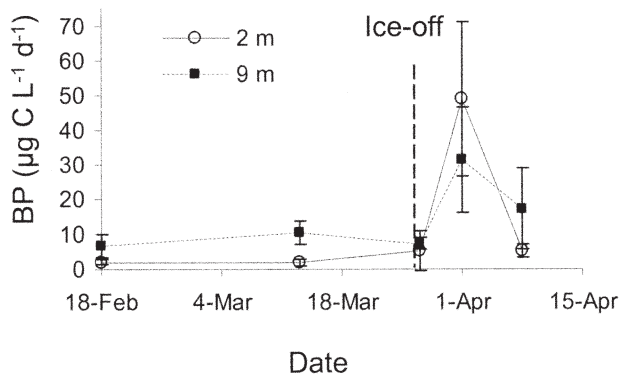


Figure 6.—Bacterial production in the epilimnion (open symbols) and hypolimnion (closed symbols) of TSL over the winter-spring transition (2003).

Chemistry

Phosphorus and NH₄⁺ concentrations were higher in the hypolimnion than the epilimnion throughout the sampling period, while NO₃⁻ concentrations were higher in the epilimnion than the hypolimnion (Table 2). Surface water SRP and NH₄⁺ concentrations decreased from 18 February to 1 April (35 to 0.1 µg P-SRP/L and 340 to 47 µg N-NH₄⁺/L), then slightly increased on 8 April (to 1.6 and 47 µg/L). At 6 m, NH₄⁺ concentrations increased over time, until a decrease on 8 April. Nitrate concentrations in the surface water increased until after ice-off (1 April), then decreased. Chloride concentrations increased with depth, reaching concentrations greater than 400 mg/L at 15 m, while sulfate concentrations decreased with depth (Table 2). Cation concentrations increased with depth, and Na⁺ was the major cation.

Nutrient concentrations in snow melt water peaked approximately 8 hrs after snow melt began (220 µg P-SRP/L, 666 µg N-NH₄⁺/L, and 1096 µg N-NO₃⁻/L), then declined (Table 1). Nutrient concentrations in rain event stream water declined

over time. No consistent patterns were observed in cation and anion concentrations during snow melt and rain events. The contribution to overall loading was greater from the snow melt event because both discharge and concentrations were higher than rain events (Table 1). Nitrate concentrations were consistently higher than NH₄⁺ or SRP. Integrating over the snow melt and rain events, combined they contributed 5.4 kg P, 40.1 kg N, and 4875 kg Cl⁻ to the lake.

Budgets

Using Cl⁻ concentrations and discharge measurements in the South Inlet, we calculated that 4126 kg Cl⁻ entered the lake during the snow melt event. However, integrating Cl⁻ concentrations measured in the lake over depth, we account for a gain of only 40.1 kg Cl⁻ over this period, in part due to loss from the lake outlet.

Snow melt delivered ~16 times more P to the epilimnion than did internal mixing to 6 m; complete mixing would have more than doubled the amount of P injected into the epilimnion over the spring summer transition period (Table 3). For the most part, nutrients delivered by snow melt were injected into the photic zone. However, on day 2, inflow density was great enough to inject approximately 1.5, 4.7 and 6.3 kg of P-SRP, N-NH₄⁺ and N-NO₃⁻ beneath the photic zone. The rain event load had a similar N to P ratio to snow melt water and, based on density calculations, was injected above 6 m depth. We calculated that nutrients delivered by snow melt runoff would support 8 times as much phytoplankton biomass as nutrients released by mixing to 6 m; complete mixing would have more than tripled phytoplankton biomass relative to mixing to 6 m. From fluorescence profiles, we calculated that on 1 and 8 April there were 91.4 and 67.7 kg C-phytoplankton in the upper 6 m of water column. Increasing the depth of mixing increased the ratio of NH₄⁺ to NO₃⁻ because NH₄⁺ is more abundant near the sediments and NO₃⁻ is more

Table 4.-Integrated Chlorophyll *a* ($\mu\text{g/L}$) at sites A and C following ice-off (27 March 2003).

Site	A			C		
Date	27 March	1 April	8 April	27 March	1 April	8 April
Integrated Chl <i>a</i>	48.3	81.1	89.0	49.4	90.0	87.6
Depth of peak (m)	1-2	1-2	3-4	1-2	2-3	3-4

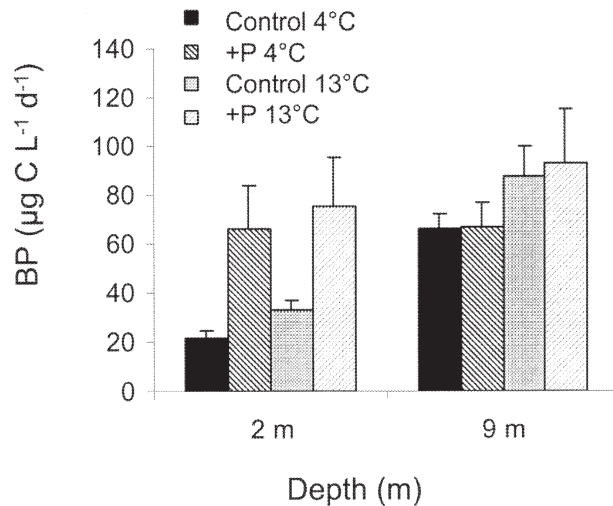


Figure 7.-Bacterial production in experimental mesocosms after three days. Treatments include P addition (hatched) and controls (solid). Each treatment was run at two temperatures (4°C (black) and 13°C (grey)) and on waters from the epilimnion (2m) and the hypolimnion (9m).

abundant higher in the water column where redox potentials are higher.

Bacteria

Bacterial production was greater at 9 m than at 2 m on all sampling dates except 1 April (Fig. 6). Prior to ice-off, mean BP at 2 m was $3.1 \mu\text{g C/L/day}$ (range 2.1 - $5.3 \mu\text{g C/L/day}$) and at 9 m was $8.1 \mu\text{g C/L/day}$ (range 6.7 to $10.4 \mu\text{g C/L/day}$). Five days after ice-off there was a large increase in BP at both 2 m and 9 m (mean values of 48.7 and $31.4 \mu\text{g C/L/day}$, respectively). After this pulse, BP decreased, but remained above pre-ice melt values (5.2 and $17.2 \mu\text{g C/L/day}$ at 2 m and 9 m, respectively). DOC concentrations remained relatively unchanged throughout the study (Table 2).

In mesocosm experiments, P addition, temperature, and depth all significantly increased BP (ANOVA, $p < 0.015$), and there was a significant interaction between depth and phosphorus ($p = 0.004$). Addition of P had a strong effect on BP in the epilimnion (rates of BP increased 204 and 130% relative to controls in 4 and 13°C treatments), but had very little effect on BP in hypolimnion waters, where rates of BP increased only 0.3 and 6% respectively (Fig. 7). Hypolimnetic BP was

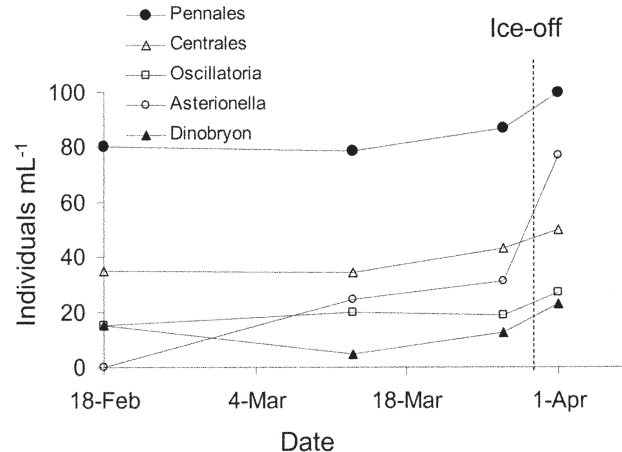


Figure 8.-Changes in phytoplankton abundances over the winter-spring transition (2003).

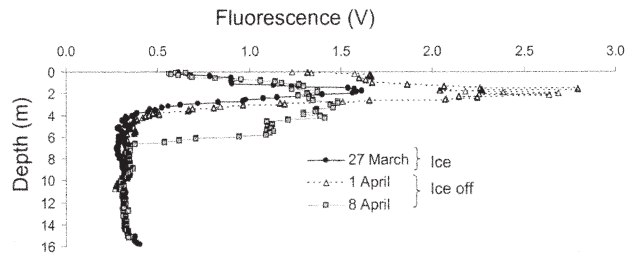


Figure 9.-Fluorescence (as an indicator of Chl *a* concentrations) with depth at site A (2003).

greater than epilimnetic BP in both controls and in the 13°C P addition, but not in the 4°C P addition. Increases in BP were roughly proportional for the four treatments in response to increased temperature.

Phytoplankton

Before ice-off, diatoms dominated the phytoplankton community, and pennate diatoms were more abundant than centric diatoms. Other abundant groups included *Oscillatoria* (*Planktothrix*) and the chrysophyte *Dinobryon* (Fig. 8). At ice-off, the Chl *a* peak at both sites A and C was between 1 and 2 m (Table 4). Chlorophyll *a* concentrations were 18% higher at site C than at site A in the surface waters (Fig. 9). Five days after ice-off, Chl *a* concentrations increased dramatically in the surface waters; total Chl *a* concentrations were 69 and 82% greater at sites A and C on 1 April compared

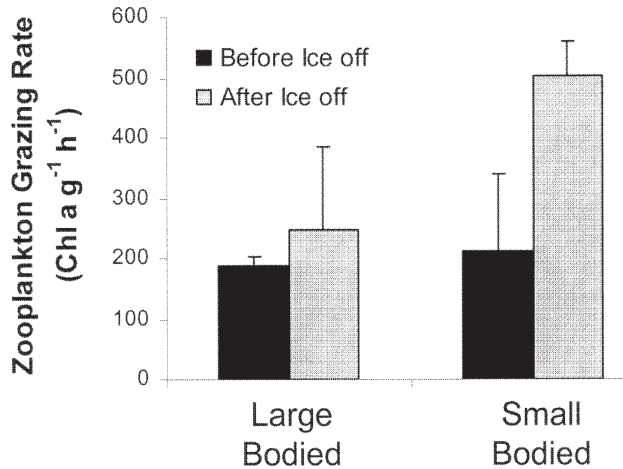


Figure 10.—Changes in zooplankton community composition over the winter to spring transition (2003). Bars indicate one standard deviation from the mean.

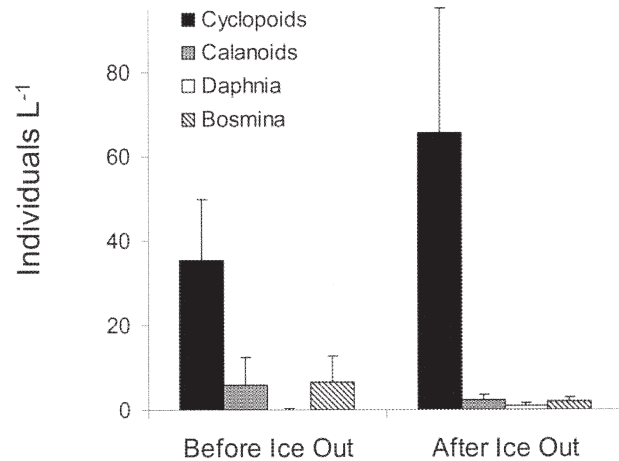


Figure 11.—Grazing rates of large and small bodied zooplankton in experimental mesocosms on phytoplankton communities collected before and after ice-off.

to 27 March. Site C had peak values 10% greater than site A, and peak concentrations occurred between 2 and 3 m. By the 8 April, Chl *a* distributions had migrated downward to 6 m and the peak concentrations occurred between 3 and 4 m. Integrated water column Chl *a* was 12% greater at site C on 1 April, but there was little difference on 8 April (Table 4).

Zooplankton

The zooplankton community was dominated by small-bodied genera before and after ice-off (Fig. 10). Under ice, cyclopoids comprised over 80% of total zooplankton density. *Bosmina* was the second most abundant genera. After ice-off, calanoid densities increased. *Daphnia* were rare throughout the study. After ice-off, *Daphnia*'s grazing rate increased by a factor of 2.8 (140 to 392 $\mu\text{g Chl } a/\text{L/g zooplankton biomass/hr}$), while small-bodied zooplankton grazing rates increased by a factor of 4.1 (153 to 627 $\mu\text{g Chl } a/\text{L/g zooplankton biomass/hr}$; Fig. 11).

Sediment Cores

Cores revealed a continuous pattern of banding with inconsistent striations between the light and dark bands as described in previous studies (Eggleton 1931, Hammer and Stoermer 1997). Core A (32 cm in length) had 58 bands ranging in thickness from 0.1 cm to 3.0 cm with an average band thickness of 0.49 cm; Core B (29 cm in length) had 42 bands, with the same range of thicknesses, but the average band thickness was 0.69 cm. Macroscopic plant parts were found throughout both cores from 16 cm to 18 cm, and in Core B they were also found at 9 cm, 19 cm, and 23.5 cm. It was difficult to assign dates to bands, because band formation in these sediments is event driven rather than annual

(Hammer and Stoermer 1997). If we assume that two organic matter bands are laid per year (corresponding to spring and fall blooms), then the 5 and 8 cm bands would correspond to ~1998, and the 17 and 17.5 cm bands would correspond to the mid to late eighties.

We found differences in diatom composition with core depth and composition (Table 5). Five genera *Cyclotella*, *Synedra*, *Stephanodiscus*, *Luticola*, and *Gyrosigma* appeared in all samples. Diatom frustules were much more common in organic bands than in clay bands. *Cymatopleura* was found in relatively high abundance only in the 5 cm clay band. *Asterionella* dominated the subsurface band (31%), while *Synedra* was most prevalent at 5 (46%) and 8 (38%) cm. *Stephanodiscus* dominated the deeper 17 and 17.5 cm samples. The pennate to centric ratio decreased with increasing core depth.

Discussion

It is clear that Cl^- concentrations have dramatically increased in the bottom waters of TSL over the last thirty years, inhibiting complete turnover in the spring. This increased water-column stability is exacerbated by increased shelter from winds, due to the conversion of the surrounding land from pasture to forest (Hammer 1995). In fact, Bridgman *et al.* (2000) estimated that lake stability increased 63% between 1981 and 1999. The changes that have occurred in TSL over the past 30 years may not be unusual for a lake of its type. Its catchment has experienced only moderate levels of development and contains a large tract of preserved woodlands immediately surrounding the lake. While the winter of 2002-2003 was unusually cold, total snowfall in the area was about average (NOAA data, Ann Arbor stations), so Cl^- inputs were likely

Table 5.-Diatom composition of sediment cores in clay and organic matter (OM) bands at 5, 8, 17, and 17.5 cm core depth. Total number (#) and relative abundance (RA) as a percent are given for the 18 most common genera.

Band type	Depth (cm)	Abundance		Cyclotella	Stephanodiscus	Asterionella	Synedra	Luticola	Gyrosigma	Fragilaria	Cymatopleura	Gymbella	Ctenophora	Diatoma	Plagiotropis	Achnanthes	Opephora	Nitzschia	Gomphonels	Amphora	Cosmonels	Other	TOTALS	Centric:Pennate		
		#	RA																							
Surf		#	47	57	100	57	11	11	1	8	0	6	0	0	0	0	0	0	0	11	0	0	0	0	322	0.477
		RA	14.6	17.7	31.1	17.7	3.4	3.4	0.3	2.5	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.4	0.0	0.0	0.0	0.0	0.0
Clay	5	#	1	16	0	4	4	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	35	0.061
		RA	2.9	2.9	0.0	45.7	11.4	11.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.7	0.0	0.0	0.0	0.0	0.0	0.0
OM	8	#	90	88	83	184	6	7	3	6	1	2	4	0	0	0	0	0	0	0	0	0	0	0	485	0.58
		RA	18.6	18.1	17.1	37.9	1.2	1.4	0.6	1.2	0.2	0.4	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Clay	17.5	#	39	51	1	33	10	4	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	141	1.765
		RA	27.7	36.2	0.7	23.4	7.1	2.8	0.0	0.0	0.0	2.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
OM	17	#	65	102	1	65	14	1	2	2	2	12	0	0	0	0	2	0	0	0	10	2	3	12	293	1.532
		RA	22.2	34.8	0.3	22.2	4.8	0.3	0.7	0.7	0.7	4.1	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	3.4	0.7	1.0	4.1	100	0.0

about average. Furthermore, much of the Cl^- that entered the lake during the snow melt event was not retained. Therefore, there is no reason to believe that TSL is unusual with respect to road salt inputs compared to other urban lakes in northern climates where road salt is commonly used. Such lakes are susceptible to the formation of a strong chemocline and, by extension, reduced seasonal mixing. This increased stability alters seasonal patterns of nutrient supply in two major ways. First, failure of spring turnover reduces the internal supply of nutrients. Total nutrient supply is therefore reduced, and the relative importance of external nutrient inputs is increased (Table 3). Second, reduced mixing will increase variability in timing and magnitude of nutrient supply to the epilimnion because melt and rain events are less predictable. Furthermore, in lakes which are not completely meromictic, large nutrient pulses will occur when turnover does occur.

Meromixis

The main causes and symptoms of meromixis (high Cl^- inputs, increased conductivity, and increased anoxia) have intensified since the last published study of TSL (Bridgeman *et al.* 2000), indicating that lake stability continues to increase. Vernal temperatures in the bottom waters were greater than 4°C (Fig. 3), a phenomenon often observed in temperate-zone lakes with high salinity in the bottom waters (Walker 1974). Specific conductivity was ~25% greater in bottom waters (1650 to 1680 $\mu\text{S}/\text{cm}$) than in surface waters (1100 to 1300 $\mu\text{S}/\text{cm}$), and Cl^- was the major contributor to the high conductivity (Table 2). Low conductivity of surface waters on 27 March was due to the melting of lake ice. A strong oxycline was present throughout the study, rising from 7 to 3 m between 18 February and 27 March, and resulting in the greatest extent of anoxia yet recorded in TSL. Despite relatively heavy winds, spring mixing was only sufficient to lower the chemocline to 6 m depth.

Chloride concentrations in the lake did not increase as much as expected based on calculations of snow melt inputs, suggesting that much (nearly 90%) of the Cl^- was not retained in the lake. If distributed evenly, Cl^- concentrations in the lake should have increased by 14.5 mg/L . One explanation for low Cl^- retention may be that the low density inflow water spread out over the lake surface and exited the lake through the outlet without mixing to depth. However, outlet flow was minimal due to low lake levels. Unfortunately, we did not sample the East Inlet during the snow melt event, and our Cl^- input calculations, therefore, underestimate total snow melt loading of Cl^- . We hypothesize that the density of snow melt runoff is higher for the East Inlet than the South Inlet and that East Inlet water is injected at deeper depths where it is retained in the lake, accumulating Cl^- in bottom waters. Although the water density of rain event runoff was lower in the East Inlet (Table 1), it is possible that snow melt runoff density is greater due to the large contribution road salt from the park-

ing lot in this small sub-catchment. A second hypothesis is that rain events throughout the growing season are important sources of Cl^- to the lake. Our rain event data showed that Cl^- concentrations were high in runoff waters, but total loads were an order of magnitude lower than the snow melt event. Still, multiple rain events occurring throughout the summer may be an important source of Cl^- to bottom waters. Later in the summer, when epilimnion waters warm and decrease in density, the density of the relatively cold and salty runoff water may be great enough that runoff is injected into deeper waters. Testing these hypotheses and more frequent sampling (especially during snow melt) of the East Inlet would improve our ability to balance the Cl^- budget in TSL.

While two other nearby lakes (First and Second Sister Lakes) experienced dramatic increases in Cl^- concentration in the sixties (Judd 1970), increased Cl^- inputs to TSL, which lies in a separate catchment, were delayed until the mid-eighties (Lehman and Naumoski 1986, Hammer 1995, Bridgeman *et al.* 2000), corresponding to the building of the nearby industrial park and parking lots that drain into the East Inlet. Since 1980, Na^+ and Cl^- concentrations in TSL have increased by a factor of approximately 20. Calcium and K^+ have doubled since 1981 (Lehman and Naumoski 1986), which is consistent with the process of cation exchange of Na^+ on clay surfaces. Surface water concentrations of SO_4^{2-} were similar in 1981 and 2003 in the surface waters, but were lower in the hypolimnion in 2003, indicating greater redox potential in the bottom waters. Magnesium and Mn^{2+} have remained relatively stable over time.

Nutrient Budgets

Reduced mixing in TSL will impact spring nutrient dynamics in two major ways: *i*) overall nutrient supply will be reduced, and *ii*) external nutrient supplies will play a greater role in controlling primary production compared to complete mixing scenarios. We calculated that incomplete mixing (to six meters only) would reduce phytoplankton production supported by internal nutrient supplies by a factor of 30 and total phytoplankton production by a factor of four compared to complete turnover during this time period (Table 3). Reduced mixing substantially increases the importance of external nutrient inputs in supporting primary productivity (from 21 to 88% of total). Although runoff waters have lower N to P ratios, overall ratios did not shift much with reduced mixing because water entrained higher in the water column has higher N to P ratios than deeper waters. With mixing to 6 m, the supply of SRP from the bottom waters was only enough to support 26% of the standing stock of phytoplankton on 1 April, and, therefore, would represent only a minor component of the annual budget. Reduced mixing would also increase the relative importance of external nutrient inputs, which would be more variable in both timing and magnitude than a relatively consistent supply of internal nutrients across years

if complete turnover occurred in the spring. The amount of snowfall, timing of snow melt, and frequency and intensity of rain events in the spring can vary from year to year and would control spring nutrient dynamics. Additionally, factors such as precipitation and anthropogenic activities in the watershed will play a greater role in controlling primary production as the importance of external nutrient supply increases.

Our results indicate that reduced mixing can also impact lake metabolism and energy flow through the microbial food web. Previous work in TSL has shown that both nutrients (Cotner and Wetzel 1992) and carbon quality (Bridgeman *et al.* 2000) influence bacterial activity. Isolation of nutrients in the bottom waters may reduce BP in the epilimnion when external nutrient supply is low. Our experiments showed that addition of SRP had no effect on hypolimnetic BP, where nutrients were not likely to be limiting, but significantly enhanced epilimnetic BP, suggesting that epilimnetic bacteria are P limited (Fig. 7). Seasonal patterns of BP over the course of our study confirm this result. BP was greater in the hypolimnion, with the exception of one date (Fig. 6). Higher BP in the epilimnion on 1 April may have been in response to nutrient inputs from snow melt runoff or a pulse of algal-derived DOC after ice-off. Curiously, BP increased in the hypolimnion as well on this date. Reduced P supply from the hypolimnion may strengthen competition between bacterioplankton and phytoplankton in the epilimnion and may reduce overall BP.

Impacts on community composition

There is evidence that meromixis affects the composition of phytoplankton, zooplankton, and benthic communities in TSL. Data from sediment cores suggest a change in phytoplankton community composition over the recent past. The most common genus in our surface sediments was *Asterionella* (Table 5), a genus found in mesotrophic freshwater to moderately brackish environments (Bradbury 1988) and often associated with increased ion concentrations due to human impacts (Dixit *et al.* 2000). Our results indicate that *Asterionella* abundance in sediments has continued to increase since the study of Hammer and Stoermer (1997) in 1994. *Asterionella* was also found in relatively high abundance in water column samples (Fig. 8), and comprised a greater portion of the total phytoplankton biomass than in 1999 (Bridgeman *et al.* 2000). The centric to pennate diatom ratio decreased from years 1994 to 2003, suggesting a shift away from eutrophic conditions (Brugam 1978, but see Stoermer and Smol 1999 for criticism of the use of this ratio). A second noticeable shift in phytoplankton community composition between 1999 and 2003 surveys is the reduction in relative abundance of *Oscillatoria* (T. Bridgeman *pers. comm.*).

The under-ice zooplankton community also differed from recent years. *Daphnia* abundances were much lower than in

1997 and 1999 (Fig. 11 T. Bridgeman, *pers. comm.*). One explanation for this shift may be that an increase in the anoxic zone may have restricted the vertical migration of *Daphnia*, preventing escape from fish predation in the fall. *Bosmina*, on the other hand, is small enough to avoid visual predation by fish (Wright 1978). Studies have found the response of primary production to nutrient pulses may be mediated by zooplankton and fish community structure (Cottingham and Schindler 2000, Strauss *et al.* 1994), and nutrient pulses may be more common under reduced mixing conditions in which storm events play a stronger role in controlling nutrient inputs. The decrease in large-bodied zooplankton will enhance the effect of these pulsed events, as the small-bodied zooplankton population will have less effect of dampening pulses of primary production. Therefore, the combination of decreased internal nutrient supply and decreased large-bodied zooplankton populations may change the lake from a relatively stable system with two major nutrient pulses (spring and fall turnover) to a storm-event driven system, with decreased dampening capacity by zooplankton on the primary production. Finally, changes in mixing regimes will alter benthic community composition as well. While we did not study the benthos, Bridgeman *et al.* (2000) noted declines in benthic invertebrate abundances and diversity in recent years.

Remediation

In this study, we show that impacts of reduced spring mixing include (1) a reduction in total nutrient supply and primary productivity during the winter to spring transition, (2) an increase in the importance of external nutrients in driving vernal levels and patterns of primary production, and (3) shifts in phytoplankton and zooplankton community composition, which may enhance the effects of external nutrient pulses. It is currently not clear whether, or when, these changes warrant remediation efforts. Below we discuss briefly the options for reversing the effects of road salt inputs.

In lakes not yet completely meromictic (*i.e.*, still experience occasional turnover events) reduction of road salt application in catchments would cause a return to baseline conditions, especially in lakes with high flushing rates. Current alternatives to NaCl as a deicer (*e.g.*, calcium magnesium acetate, potassium acetate, and verglinit), however, are either costly (CMA is ~ 25 times more costly than NaCl) or have similar environmental impacts.

Active remediation of impaired lakes would require oxygenation of the hypolimnion and desalinization. Artificial hypolimnetic oxygenation (in concert with alum addition to reduce P concentrations) has been applied to restore eutrophied lakes (*e.g.*, Dokes *et al.* 1986, Bonsdorff and Storberg 1990). The pumping of O₂ below the chemocline could facilitate mixing and relieve the effects of anoxia. Once turnover occurs, out-

flow would reduce salinity, and thus induced mixing could be used to dilute lake Cl⁻ levels. Desalinization, however, would require many years. Using average precipitation values for a two week mixing period in April and a one month mixing period in November, we calculated that it would take about eight years to eliminate the Cl⁻ accumulated in the bottom waters of TSL. For this calculation, we assumed *i*) a runoff coefficient of 0.2 (based on catchment characteristics, McCuen 1998) and *ii*) that Cl⁻ left the lake only during mixing periods. Drops in Cl⁻ concentration due to artificial mixing could return the lake to more frequent natural turnover dynamics. Bottom water withdrawal would accelerate the desalinization process. However, without reductions of salt inputs, artificial turnover and desalinization processes would require a long-term management program. Once terminated, salt inputs would likely cause the lake to return to a state of meromixis.

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