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Volcanic heat flux and short-term holomixis during the summer stratification period in a crater lake

Abstract—We sampled Lake Katanuma from 1998 to 2002 at weekly or biweekly intervals, except in winter. This dimictic volcanic lake has a pH of 2.0–2.2. In summer, volcanic heat at the lake bottom results in a small water temperature difference of 3–7°C between the epilimnion and hypolimnion. During the April–August stratification period in 1998, 1999, and 2002, the entire water column mixed for 1–8 d, when air temperature declined 4–8°C from the epilimnion temperature. During these mixing events, anoxic, hydrogen sulfide–rich water from the hypolimnion spread over the entire lake. In contrast, distinct short-term turnover did not occur during the stratification period in 2000 or 2001. However, the early onset of autumn turnover in August 2000 and 2001 caused anoxic conditions with negative Eh values to persist for ~2 weeks throughout the entire water column. Volcanic heat flux from the lake bottom fluctuated from 29.0 to 35.8 W m^{-2} from year to year. The frequency and duration of short-term holomixis thus depended on interannual variations in volcanic heat flux and weather.

Many temperate-zone lakes have monomictic or dimictic stratification and circulation patterns, although patterns can vary in individual lakes. In general, the final water temperature during the spring turnover determines the initial hypolimnion temperature of dimictic lakes; the hypolimnetic temperature changes little throughout the summer stratification period. In contrast, the epilimnion temperature rises during the transition from spring to summer, thus increasing the stability of stratification throughout the heating season in many dimictic lakes (Wetzel 2001). Factors such as basin configuration, surface area, climatic variations, inflow, and high chemical concentrations can modify thermal stratification (Jellison and Melack 1993; Chapman et al. 1998; Rodrigo et al. 2000; Ford et al. 2002). The volcanic heat supply of crater lakes also affects thermal stratification (McManus et al. 1993; Takano et al. 1994; Crawford and Collier 1997). In some crater lakes, lake water temperature exceeds ambient temperature because of the large geothermal heat flux from the lake bottom, and the heat flux may change in accordance with volcanic activity (Brown et al. 1989; Rowe et al. 1992; Ohba et al. 1994; Pasternack and Varekamp 1997).

Lake Katanuma in the Naruko volcanic crater in northern Japan receives a volcanic heat supply from the lake bottom (Satake and Saijo 1973; Satake 1975; Sato 1995). Satake and Saijo (1978) reported that Lake Katanuma was dimictic, but that because of the heat supply, the temperature difference between the epilimnion and hypolimnion was 3–5°C during the stratification period, and that autumn turnover generally occurred earlier than in typical temperate-zone lakes. However, the frequency of their observations at Lake Katanuma was limited, and because no data were consistently obtained over a year on a monthly or bimonthly basis, they had to synthesize the seasonal changes in limnological features by using data derived from rather fragmentary observations in different years. The lack of frequent, continuous observations limited their interpretation of seasonal changes and estimations of environmental factors. By conducting weekly or biweekly limnological surveys at Lake Katanuma from 1998 to 2002 in all seasons except winter, the present study obtained the frequent and continuous temperature and environmental data required for accurate estimation and interpretation of interannual variation. We also examined factors affecting stratification stability between spring and summer, including the degree of heat flux from the lake bottom and weather conditions.

Lake Katanuma is a volcanic lake that is located in northern Miyagi Prefecture, Japan (38°44.0′N, 140°43.5′E) at an altitude of 306 m above sea level. The lake has a surface area of 1.24×10^5 m^2, a volume of 6.89×10^5 m^3, a maximum depth of 21 m (Fig. 1), a catchment area of 4.58×10^5 m^2, and no surface overflow. The water is highly acidic (pH = 2.0–2.2). Subaqueous fumaroles inject sulfur-containing gases, such as hydrogen sulfide, into the lake water, and volcanic heat emerges from the lake bottom (Satake 1975; Sato 1995).

Sampling was carried out on a weekly or biweekly basis from 1998 to 2002, except during the winter months. Samples were taken within 1 h of 1100 h to avoid diel changes. All samples were taken from a sampling station moored at the deepest point, near the lake center, except those for 28 March 2000 and 21 March and 26 December 2001, when ice several centimeters thick covered the lake center. A Van Dorn water sampler collected 3-liter samples at seven different depths (0, 1, 2, 4, 6, 10, and 15 m). Dissolved oxygen was determined by Winkler's method as modified by Strickland and Parsons (1972). Hydrogen sulfide was measured by using a No. 211 detector tube (Gastec), and pH was determined with a pH digital meter (UC-23, Central Kagaku). The concentration of sulfate was analyzed with an ion chromatograph (DX-120, Nippon Dionex). Temperature, oxidation–reduction potential (ORP), and conductivity were determined in situ at depths of 0, 1, 2, 3, 4, 5, 6, 8, 10, 13, and 15 m. Temperature was measured with a thermometer (SK-1250MC, Sato Keiryoki) from February 1998 to May 2000, and with a U-22 water-quality monitor (Horiba) from May

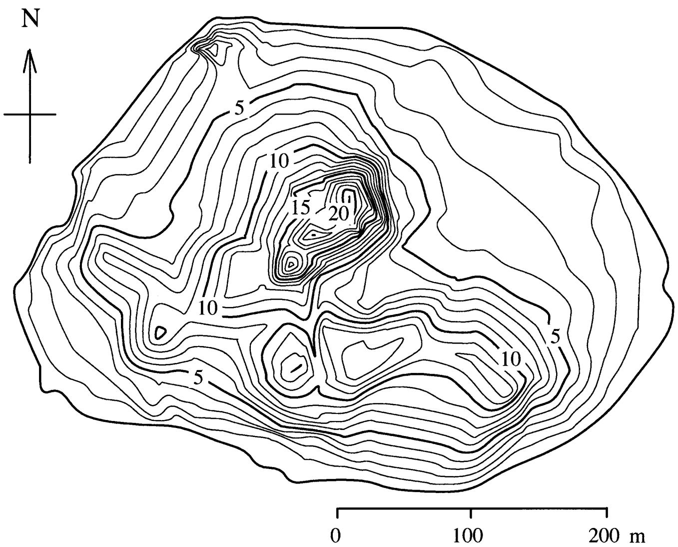

Fig. 1. Bathymetric map of Lake Katanuma (measured on 11 April 2002). Depths are shown in meters.

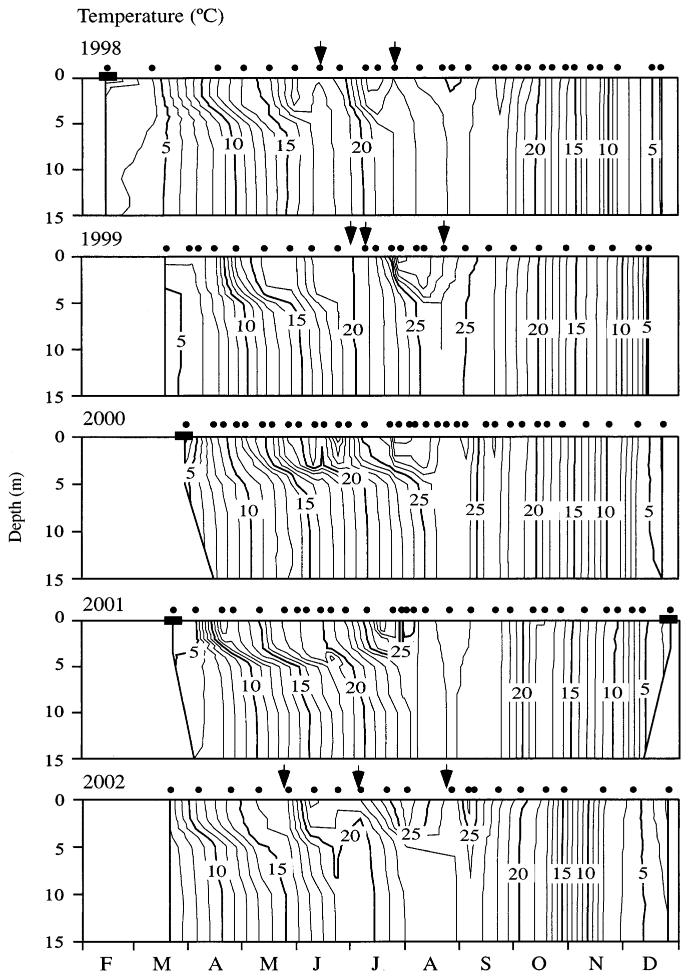

Fig. 2. Depth–time diagrams for water temperature in Lake Katanuma from 1998 to 2002. Thick lines represent ice cover. Arrows and dots above the upper horizontal axis indicate the short-term holomixis and sampling days, respectively.

2000 to December 2002. From May 2000, ORP and conductivity also were measured with the water-quality monitor. Temperature loggers recorded long-term continuous measurements of water temperature at 30-min intervals in the lake center (StowAway TidbiT, Onset Computer). Measurements began at depths of 1 and 6 m in September 1998 and were continued at depths of 4 and 10 m from June 1999 to December 2002.

Seasonal water temperature changes in Lake Katanuma were essentially dimictic because of the formation of winter ice cover (Fig. 2). Stratification with a thermocline depth of 3–5 m was formed from April to August except in 2001. Autumn turnover occurred in late July in 2001, whereas autumn circulation began in late August or early September in the other years. The temperature differences between the epilimnion and hypolimnion during stratification periods were as small as 3–7°C. Furthermore, we observed mixing of the entire lake water for 1–8 d several times during the stratification period in 1998, 1999, and 2002. Short-term turnover from the surface to the bottom was observed at least twice (12 June and 24 July) in 1998. As determined by temperature loggers, which recorded almost the same temperatures at depths of 1, 4, 6, and 10 m, short-term holomixis occurred on 30 June, 9 July, and 15 August 1999 and 18 May, 25 June, and 18 August 2002. In contrast, short-term turnover was not observed during the stratification periods in 2000 and 2001. Over the 5 yr of the observations, the frequency of short-term holomixis events varied from year to year. The full data set for temperatures is available in Web Appendix 1 at http://www.aslo.org/lo/toc/vol_49/issue_6/2287a1.html.

Lake-bottom surface temperatures in the central, southern, and northeastern areas of Lake Katanuma are 4–10°C higher than bottom water temperatures (Sato 1995). The lake's volcanic heat supply increases the hypolimnion temperature during stratification periods, whereas the epilimnion prevents heat loss to the atmosphere. We compared the increase in water temperature at 10 m in the hypolimnion during a period of stratification to estimate the interannual variability of volcanic heat supply. The water temperature in the hypolimnion increased linearly from early spring to the onset of the short-term holomixis. The regressions between temperature and day of the year were $T = -9.89 + 0.171D$ ($n = 4$, $r^2 = 1.000$) for 1998, $T = -11.61 + 0.174D$ ($n = 6$, $r^2 = 0.999$) for 1999, $T = -9.20 + 0.152D$ ($n = 13$, $r^2 = 0.998$) for 2000, $T = -10.82 + 0.164D$ ($n = 13$, $r^2 = 0.999$) for 2001, and $T = -5.29 + 0.142D$ ($n = 8$, $r^2 = 1.000$) for 2002, where T is the temperature at 10 m and D is day of the year.

The daily rate of increase of the water temperature in the hypolimnion ranged from 0.142°C to 0.174°C d^{-1} (Table 1). Statistical analyses with t-tests indicated significant rate differences ($p < 0.01$) between all years except 1998 and 1999 ($p > 0.10$), and 1998 and 2001 ($0.05 < p < 0.10$). Temperature loggers moored at 10 m recorded similar daily rate increases (0.150°C, 0.167°C, and 0.143°C d^{-1} in 2000, 2001, and 2002, respectively). Because the rate increases in 1998 and 1999 exceeded those in 2000 and 2001, epilimnion and hypolimnion temperature differences in 1998 and 1999 were as small as 3–5°C, and short-term holomixis occurred easily.

Table 1. Increasing water temperature rate in the hypolimnion, hypolimnetic area and volume, and heat flux from the bottom to the water in Lake Katanuma.

Year	Rate of increase of water temperature (°C d^{-1})	Level* (cm)	Area† ($\times 10^4$ m^2)	Volume‡ ($\times 10^5$ m^3)	Hear flux (W m^{-2})
1998	0.171	−27	5.40	2.24	34.4
1999	0.174	5	5.69	2.42	35.8
2000	0.152	14	5.79	2.47	31.4
2001	0.164	−10	5.55	2.34	33.5
2002	0.142	−8	5.57	2.35	29.0

* Relative differences in the average elevation during the stratification period from standard bathymetric elevation data (Fig. 1).
† Hypolimnetic area at a depth of 5 m.
‡ Hypolimnetic volume.

Although 2002 had the lowest rate increases, ice breakup and stratification formation occurred 20 d earlier than in other years. Consequently, the hypolimnion water temperature in 2002 was high enough for mixing to occur earlier than in other years. Thus, the rate of hypolimnetic temperature increase and the starting date of stratification determined the occurrence of short-term holomictic events.

Two main factors affect the rate of water temperature increase in the hypolimnion: volcanic heat flux from the lake bottom and volume of the hypolimnion. The volume of the hypolimnion is determined by the depth of the lower metalimnion–upper hypolimnion boundary and the lake surface elevation. In Lake Katanuma, the latter fluctuated within 100 cm from 1998 to 2002. Assuming that the upper hypolimnion was 5 m in depth, the annual hypolimnion volume was estimated from bathymetric data (Fig. 1), with compensations made for the average surface elevation during the stratification period. Heat flux from the lake bottom was calculated with the assumption that the density of lake water equaled unity and that direct solar inflow and heat loss by conductive flux to the metalimnion and seepage could be neglected. Volcanic heat fluxes ranged from 29.0 to 35.8 W m^{-2} (Table 1).

In 1989, Sato (1995) estimated a heat flux of 15.6 W m^{-2} at Lake Katanuma. This value is almost one half of our estimates. Although Sato's smaller value might reflect a decline in volcanic activity in 1989, the value also may have been underestimated, because it was calculated from differences in hypolimnetic temperatures at only two points over a period of 48 d. If a short-term holomictic event occurred during those 48 d, cooling caused by mixing in the hypolimnion could have led to underestimation of temperatures.

The amount of heat flux determines the stratification pattern of crater lakes. Although Crater Lake, the deepest lake in the United States, tends to have incomplete deep-water ventilation, a small flux of hydrothermal heat (0.9–1.2 W m^{-2}) produces instabilities in the density structure that may drive deep-lake mixing (McManus et al. 1993). Pasternack and Varekamp (1997) pointed out that the steady-state temperatures of perfectly mixed crater lakes are determined mainly by the magnitude of the volcanic heat influx relative to the lake surface area. Lake Yugama in Japan, which receives a hydrothermal heat flux of 3–10 MW, had water temperatures 9°C higher than ambient air temperatures over the entire period from 1988 to 1989. Heat flux values for Lake Yugama increased to 19–25 MW and the difference between the water and ambient temperatures reached 12°C in 1990, which corresponded to volcanic activity (Ohba et al. 1994). Water temperatures of 40–60°C have been recorded in the hot crater lake at Volcán Poás, Costa Rica, which outputs a baseline energy flux of approximately 200 MW (Brown et al. 1989; Rowe et al. 1992). The total volcanic heat input for Lake Katanuma ranges from 3.6 to 4.4 MW, as estimated by multiplying the heat flux per unit area (Table 1) and the lake surface area. If Lake Katanuma were to receive larger heat fluxes than at present, the lake could destratify at other times.

When the water temperature of the epilimnion declines to that of the hypolimnion during the stratified period, short-term holomictic turnover begins. To estimate the major factors driving the decrease in epilimnetic temperature, we estimated the heat flux of epilimnetic water on the onset days of short-term holomictic events and 2 d before mixing by using a box model (Rowe et al. 1992; Ohba et al. 1994; Pasternack and Varekamp 1997). The heat budget of the epilimnion during the stratification period is given by

$$E_{epil} = E_{rad} + E_{rain} + E_{evap} + E_{cond} + E_{sun} + E_{vol}$$

where E_{epil} is the rate of change in the heat energy of the epilimnion, and E_{rad}, E_{rain}, E_{evap}, E_{cond}, E_{sun}, and E_{vol} are the radiative heat flux, the heat inflow due to rain water, the evaporative heat loss, the conductive heat flux, the solar heat influx, and the volcanic heat inflow from the bottom under the epilimnion, respectively. Heat fluxes entering the epilimnion are defined as positive and fluxes leaving the epilimnion are defined as negative. The heat loss due to seepage and the flux to the hypolimnion by conduction were assumed to be sufficiently small and were neglected. The daily rates of E_{rad} were calculated from the equation used by Ohba et al. (1994) and the rates of E_{rain}, E_{evap}, E_{cond}, and E_{sun} were calculated from the equations adopted by Pasternack and Varekamp (1997). The rate of E_{vol} was estimated by multiplying the epilimnetic bottom area by the volcanic heat flux for the respective year. Although the temperatures of ambient air, lake water, and the lake surface are needed for the calculation, the temperature of the lake surface water was not recorded. Therefore, we used the daily average temperature at 1 m depth for both the lake water and lake surface temperatures. Data on daily precipitation, average wind speed, and insolation duration were from the database of the Japan Meteorological Agency (http://www.jma.go.jp/). These data were recorded by the Automated Meteorological Data Acquisition System (AMeDAS) at Kawatabi (38°44.6′N, 140°45.6′E), which is situated 3.2 km east of Lake Katanuma.

Table 2 shows that on a sunny day (16 May 2002), the estimated solar heat influx (E_{sun}) exceeded the total heat loss ($E_{rad} + E_{rain} + E_{evap} + E_{cond}$), although the air temperature was lower than the water temperature. By contrast, the daily heat fluxes from the epilimnion were estimated to be −9.02 to −23.43 MW when the temperature difference between the epilimnetic water and ambient air exceeded 3.7°C and the insolation duration was shorter than 0.5 h. Such heat losses

Table 2. Heat flux of epilimnetic water on the days of onset of short-term holomictic events and 2 d before mixing when using a box model.

Date	T_1 (°C)	T_a (°C)	Precipitation† (mm)	Wind speed† (m s^{-1})	Insolation duration† (h)	E_{rad} (MW)	E_{rain} (MW)	E_{evap} (MW)	E_{cond} (MW)	E_{sun} (MW)	E_{vol} (MW)	E_{epil} (MW)
28 Jun 1999	21.5	19.8	0	1.5	4.5	−1.08	0	−2.40	−1.02	4.20	2.40	2.09
29 Jun	21.2	17.4	5	2.4	0	−2.37	−0.42	−7.58	−3.37	0	2.40	−11.34
30 Jun*	20.6	16.0	68	2.6	—‡	−2.91	−7.02	−5.95	−4.51	—	2.40	−18.00
07 Jul 1999	21.6	17.5	0	1.6	3.7	−2.57	0	−6.63	−2.89	3.45	2.40	−6.24
08 Jul	21.7	17.5	0	2.0	2.8	−2.66	0	−7.83	−3.40	2.61	2.40	−8.87
09 Jul*	21.4	17.0	0	1.3	0.5	−2.78	0	−6.43	−2.89	0.47	2.40	−9.20
13 Aug 1999	27.9	24.0	81	2.8	0	−2.63	−7.00	−12.31	−3.88	0	2.40	−23.43
14 Aug	26.8	22.6	41	3.2	0.2	−2.78	−3.79	−13.65	−4.59	0.19	2.40	−22.23
15 Aug*	26.1	22.4	53	3.5	0	−2.46	−4.35	−12.49	−4.30	0	2.40	−21.20
16 May 2002	15.7	11.8	0	1.8	12.2	−2.35	0	−4.94	−2.98	11.38	1.98	3.08
17 May	15.3	8.4	9	1.1	0	−4.04	−1.38	−6.76	−4.51	0	1.98	−14.70
18 May	14.8	10.7	44	0.8	0	−2.43	−4.02	−3.32	−2.14	0	1.98	−9.93
23 Jun 2002	19.6	11.6	5	1.3	0	−4.87	−0.89	−10.78	−5.78	0	1.98	−20.33
24 Jun	19.6	14.6	0	1.4	4	−3.13	0	−7.03	−3.48	3.37	1.98	−7.93
25 Jun*	19.2	11.0	1	1.2	0	−4.92	−0.18	−11.96	−5.69	0	1.98	−20.77
16 Aug 2002	24.7	20.0	3	1.0	0	−3.09	−0.32	−7.35	−2.77	0	1.98	−11.55
17 Aug	24.3	19.0	1	0.5	0	−3.43	−0.12	−6.49	−2.52	0	1.98	−10.57
18 Aug*	24.2	21.3	1	0.4	0	−1.92	−0.06	−3.04	−1.14	0	1.98	−4.17

T_1 and T_a are the average temperatures of the lake (1-m depth) and ambient air, respectively.
* The days of onset of short-term holomictic events.
† Data from the Japan Meteorological Agency database. The precipitation, wind speed, and insolation duration data were recorded by AMeDAS at Kawatabi (38°44.6′,N 140°45.6′E), which is situated 3.2 km east of Lake Katanuma.
‡ No data.

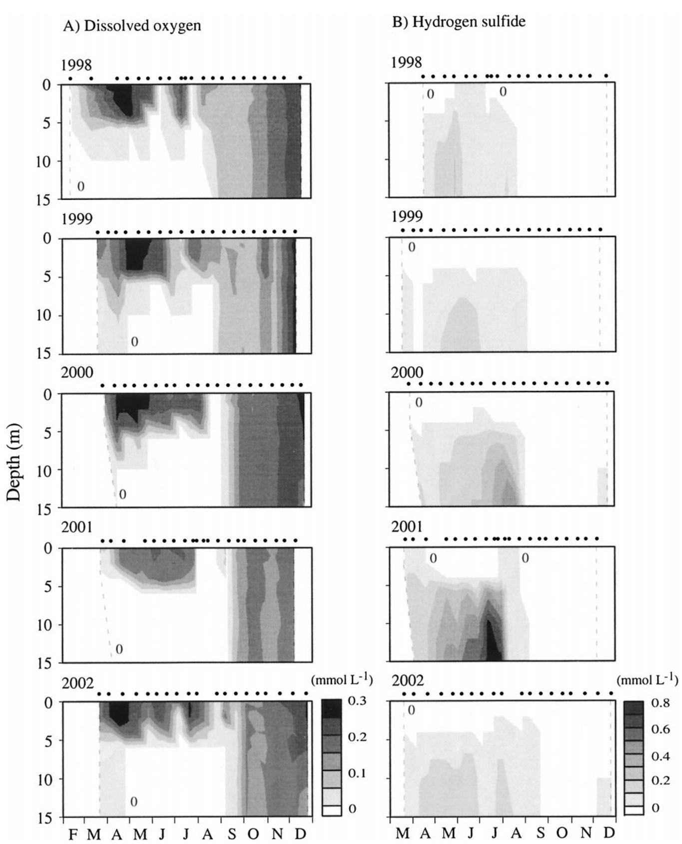

Fig. 3. Depth–time diagrams for (A) dissolved oxygen and (B) hydrogen sulfide concentrations in Lake Katanuma from 1998 to 2002. Dots above the upper horizontal axis indicate sampling days.

could cause a temperature decrease of 0.42–1.07°C d^{-1} in the epilimnetic and metalimnetic water. Table 2 also shows that rainfall and wind could contribute to heat loss from the lake surface by increasing the values E_{rain} and E_{evap}, respectively.

The stability of stratification in Lake Katanuma depends on three factors: volcanic heat flux from the lake bottom, the timing of ice breakup, and weather conditions (mainly insolation duration and decreases in air temperature) between spring and summer. Thus, thermal discontinuity varies greatly from year to year in relation to volcanic activities and weather conditions.

The vertical distribution of dissolved oxygen and hydrogen sulfide varied with seasonal changes in lake water stratification and circulation (Fig. 3). The full data set of dissolved oxygen and hydrogen sulfide is available in Web Appendix 2 at http://www.aslo.org/lo/toc/vol_49/issue_6/2287a2.html. During the stratification period from April to August, oxic water with no hydrogen sulfide was detected in the epilimnion, whereas oxygen depletion and accumulated hydrogen sulfide were prominent in the hypolimnion. In the stratification period of 1998, short-term holomixis led to oxygen depletion and the spread of hydrogen sulfide throughout the water column. Decreases in dissolved oxygen in the upper layer and in hydrogen sulfide in the hypolimnion also were observed after short-term holomixis in 1999 and 2002. In contrast, hydrogen sulfide gradually accumulated in the hypolimnion from April to August in both 2000 and 2001. Maximum concentrations reached 0.53 and 0.73 mmol L^{-1} in 2000 and 2001, respectively. Furthermore, when autumn turnover began, the hydrogen sulfide accumulated in the hypolimnion oxidized and the dissolved oxygen was completely consumed. Anoxic conditions from the surface to the bottom then continued for ~2 weeks. Anoxic conditions and hydrogen sulfide disappeared completely in the entire water column during the autumn circulation period.

After the short-term holomixis, hydrogen sulfide that had accumulated in the hypolimnion was oxidized to sulfur and the lake water changed to a pale white color due to the suspension of sulfur particles: $2H_2S + O_2 \rightarrow 2S + 2H_2O$. The amount of accumulated hydrogen sulfide was 1.26×10^8 mol calculated from the average concentration and hypolimnetic volume on 26 July 2001, which was 3 d before the onset of early autumn turnover in 2001. By contrast, there were 0.56×10^8 mol of dissolved oxygen in the epilimnion. Because the oxidation of 1 mol of hydrogen sulfide requires 0.5 mol of oxygen, the accumulated hydrogen sulfide could have completely consumed the dissolved oxygen in the epilimnion. Conversely, the accumulated hydrogen sulfide 10–14 d before the autumn turnover in August 2000 and during short-term mixing in June and July 1998 was 0.68×10^8, 0.42×10^8, and 0.18×10^8 mol, respectively, and would have consumed only 44%, 32%, and 13% of the dissolved oxygen in the epilimnion. However, these low values may reflect the time lags between the sampling day and the day on which mixing occurred, during which hydrogen sulfide might have accumulated in higher concentrations.

Although the pH of the water in Lake Katanuma ranged from 2.0 to 2.2, high densities of chironomid larvae (*Chironomus acerbiphilus*), benthic algae (*Pinnularia acidojaponica*), and planktonic algae (*Chlamydomonas acidophila*) often have been observed (Satake and Saijo 1974; Doi et al. 2001, 2003*a,b*). After the short-term holomixis or the early autumn turnover had occurred, the acute influence of anoxic and hydrogen sulfide–rich conditions on chironomid larvae was observed. Almost all sedentary larvae, that is, those distributed in the sediments covered by the epilimnetic water during the stratification period, swam into the surface water and the density of larvae sometimes became so high that parts of the lake surface appeared red. Most larvae were transported to the lakeshore and finally died because of oxygen depletion or hydrogen sulfide toxicity. We observed this phenomenon on a massive scale on 12 June 1998 and 29 July 2001. The larval population density decreased markedly immediately after the short-term holomixis or early autumn turnover with anoxic, hydrogen sulfide–rich conditions. However, unlike the Lake Nyos CO_2 gas disaster in Cameroon (Kling et al. 1987; Sigvaldason 1989), the Lake Katanuma phenomenon has not yet affected human health.

Surface waters had Eh values of ~500 mV, although sharp declines in Eh were observed during stratification periods. Maximum Eh gradients exceeded -400 mV m^{-1} between depths of 3–4 m in 2000 and 4–5 m in 2001 and 2002. Negative Eh values below -100 mV were recorded in the hypolimnion, especially when hydrogen sulfide accumulated. During the autumn turnover period, Eh values of ~450 mV remained homogeneous throughout the entire water column. Conductivity ranged from 0.22 to 0.42 S m^{-1} and averaged 0.305 S m^{-1}. This conductivity was due mainly to the high concentration of sulfate, which ranged from 1.69 to 5.00 mmol L^{-1}, with a mean concentration of 3.96 mmol L^{-1}. The full data set of ORP and conductivity is available in Web Appendix 3 at http://www.aslo.org/lo/toc/vol_49/issue_6/2287a3.html.

The density difference per degree lowering of water temperature at 15°C and 20°C is 0.14 and 0.21 kg m^{-3}, respectively (Vallentyne 1957), whereas the estimated density differences between the epilimnion and hypolimnion due to chemical stratification were 0.037–0.047 kg m^{-3} calculated from the 0.47–0.58 mmol L^{-1} differences in sulfate concentration (Chen and Millero 1986) between the two layers during spring in 2000. A comparison of the density differences between the epilimnion and hypolimnion due to thermal versus chemical stratification indicated that thermal stratification predominated in Lake Katanuma.

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Clearance of aquatic hyphomycete spores by a benthic suspension feeder

Abstract—We placed individual *Elliptio complanata* in aerated suspensions of conidia (asexual spores) of aquatic hyphomycetes (Fungi). Mussels actively ingested conidia at an initial rate of over 20,000 h^{-1}. The conidia of the seven most common species were removed at different rates, but there was no consistent correlation between conidial size or shape (tetraradiate, sigmoid, or clove shaped) and removal by *E. complanata*. At the maximum clearance rate, animals ingested the equivalent of 159 ng conidial biomass h^{-1}, corresponding to 4.7 $\mu g\ d^{-1}\ g^{-1}$ animal dry mass. At natural densities, *E. complanata* may be able to eliminate a considerable proportion of the conidial production, causing a shift in the proportions of species in the remaining conidia.

In small woodland streams, leaves of riparian trees often dominate the food supply (Allan 1995). They are rapidly colonized by a specialized group of fungi, aquatic hyphomycetes, the growth and activity of which render the substrate more attractive to leaf-eating invertebrates (shredders; Bärlocher 1985; Suberkropp 1992). Aquatic hyphomycete biomass on decaying leaves may reach 17% of total detrital mass (Gessner 1997), and fungal production per unit area in a small, nutrient-poor stream is of the same order of magnitude as that of bacteria and invertebrates (Suberkropp 1997). Several studies estimated that close to 50% of total fungal production is channeled into conidia (asexual spores; Findlay and Arsuffi 1989; Suberkropp 1991; Sridhar and Bärlocher 2000). Up to eight conidia may be released per microgram of detrital mass per day (Gessner 1997), adding up to a total spore concentration approaching 30,000 L^{-1} stream water in late fall (Iqbal and Webster 1973). Gessner (1997) estimates that 20 g of conidial mass pass daily through a cross-section of a small stream (discharge of 60 L s^{-1}). Nothing is known about the fate of this component of fine particulate organic matter (FPOM).

The Eastern elliptio, *Elliptio complanata* (Lightfoot), is a freshwater bivalve (Unionidae) found in ponds and streams along the Atlantic seaboard of North America from the Carolinas to the St. Lawrence River Basin and westward to Lake Superior. This benthic suspension feeder occurs in densities of up to 150 animals m^{-2} (Fisher and Tevesz 1976). It takes in large volumes of water through an incurrent siphon and clears all particles exceeding 1.6 μm in diameter (Paterson

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