Division of Geological & Geophysical Surveys

Report of Investigations 2011-6
version 2

SUMMIT CRATER LAKE OBSERVATIONS, AND THE LOCATION, CHEMISTRY, AND pH OF WATER SAMPLES NEAR MOUNT CHIGINAGAK VOLCANO, ALASKA: 2004–2011

by
Janet R. Schaefer, William E. Scott, William C. Evans,
Bronwen Wang, and Robert G. McGimsey

Chiginagak volcano as viewed from the shore of Mother Goose Lake. Photo by Willie Scott (USGS), August 20, 2004.

September 2013

Released by

STATE OF ALASKA
DEPARTMENT OF NATURAL RESOURCES
Division of Geological & Geophysical Surveys
3354 College Rd., Fairbanks, Alaska 99709-3707

$13.00

STATE OF ALASKA
Sean Parnell, *Governor*

DEPARTMENT OF NATURAL RESOURCES
Joe Balash, *Acting Commissioner*

DIVISION OF GEOLOGICAL & GEOPHYSICAL SURVEYS
Robert F. Swenson, *State Geologist and Director*

Publications produced by the Division of Geological & Geophysical Surveys (DGGS) are available for free download from the DGGS website (www.dggs.alaska.gov). Publications on hard-copy or digital media can be examined or purchased in the Fairbanks office:

Alaska Division of Geological & Geophysical Surveys
3354 College Rd., Fairbanks, Alaska 99709-3707
Phone: (907) 451-5020 Fax (907) 451-5050
dggspubs@alaska.gov
www.dggs.alaska.gov

Alaska State Library
State Office Building, 8th Floor
333 Willoughby Avenue
Juneau, Alaska 99811-0571

Alaska Resource Library & Information Services (ARLIS)
3150 C Street, Suite 100
Anchorage, Alaska 99503

Elmer E. Rasmuson Library
University of Alaska Fairbanks
Fairbanks, Alaska 99775-1005

University of Alaska Anchorage Library
3211 Providence Drive
Anchorage, Alaska 99508

CONTENTS

TABLES

FIGURES

SUMMIT CRATER LAKE OBSERVATIONS, AND THE LOCATION, CHEMISTRY, AND pH OF WATER SAMPLES NEAR MOUNT CHIGINAGAK VOLCANO, ALASKA: 2004–201

version 2

by

Janet R., Schaefer[1], William E. Scott[2], William C. Evans[3], Bronwen Wang[4], and Robert G. McGimsey[5]

INTRODUCTION

Mount Chiginagak is a hydrothermally active volcano on the Alaska Peninsula, approximately 170 km south–southwest of King Salmon, Alaska (fig. 1). This small stratovolcano, approximately 8 km in diameter, has erupted through Tertiary to Permian sedimentary and igneous rocks (Detterman and others, 1987). The highest peak is at an elevation of 2,135 m, and the upper ~1,000 m of the volcano are covered with snow and ice. Holocene activity consists of debris avalanches, lahars, and lava flows. Pleistocene pyroclastic flows and block-and-ash flows, interlayered with andesitic lava flows, dominate the edifice rocks on the northern and western flanks. Historical reports of activity are limited and generally describe "steaming" and "smoking" (Coats, 1950; Powers, 1958). Proximal tephra collected during recent fieldwork suggests there may have been limited Holocene explosive activity that resulted in localized ash fall. A cluster of fumaroles on the north flank, at an elevation of ~1,750 m, commonly referred to as the "north flank fumarole" have been emitting gas throughout historical time (location shown in fig. 2). The only other thermal feature at the volcano is the Mother Goose hot springs located at the base of the edifice on the northwestern flank in upper Volcano Creek, at an elevation of ~160 m (fig. 2, near sites H1, H3, and H4).

Sometime between November 2004 and May 2005, a ~400-m-wide, 100-m-deep lake developed in the snow- and ice-filled summit crater of the volcano (Schaefer and others, 2008). In early May 2005, an estimated 3 million cubic meters (3×10^6 m^3) of sulfurous, clay-rich debris and acidic water exited the crater through tunnels at the base of a glacier that breaches the south crater rim. More than 27 km downstream, these acidic flood waters reached approximately 1.3 m above normal water levels and inundated a fertile, salmon-spawning drainage, acidifying the entire water column of Mother Goose Lake from its surface waters to its maximum depth of 45 m (resulting pH ~2.9), and preventing the annual salmon run in the King Salmon River. A simultaneous release of gas and acidic aerosols from the crater caused widespread vegetation damage along the flow path.

Since 2005, we have been monitoring the crater lake water that continues to flow into Mother Goose Lake by collecting surface water samples for major cation and anion analysis, measuring surface-water pH of affected drainages, and photo-documenting the condition of the summit crater lake. This report describes water sampling locations, provides a table of chemistry and pH measurements, and documents the condition of the summit crater between 2004 and 2011. In September 2013, the report was updated with results of water-chemistry samples collected in 2011 and 2012, which were added as an addendum.

DESCRIPTION OF WATER SAMPLE SITES

Beginning in 2005, water samples were collected near Chiginagak volcano in both acid-flood affected and unaffected streams and lakes (fig. 2). Mother Goose hot-springs water, not directly associated with the crater lake outflow, was also collected (fig. 2 sites H1, H3, and H4). Annotated photographs of each site are provided in figures 3–18. In all water-sample site photos, arrows indicate the direction of water flow. Table 1 lists the latitude, longitude, and description of each water sample location.

[1]Alaska Division of Geological & Geophysical Surveys—Alaska Volcano Observatory, 3354 College Rd., Fairbanks, Alaska 99709-3707; janet.schaefer@alaska.gov

[2]David A. Johnston Cascades Volcano Observatory, U.S. Geological Survey, 1300 SE Cardinal Court, Suite 100, Vancouver, Washington 98683

[3]Water Resources Discipline, U.S. Geological Survey, 345 Middlefield Road, Mail Stop 434, Menlo Park, California 94025

[4]Alaska Science Center, U.S. Geological Survey, 4200 University Drive, Anchorage, Alaska 99508

[5]Alaska Volcano Observatory, Volcano Science Center, U.S. Geological Survey, 4200 University Drive, Anchorage, Alaska 99508

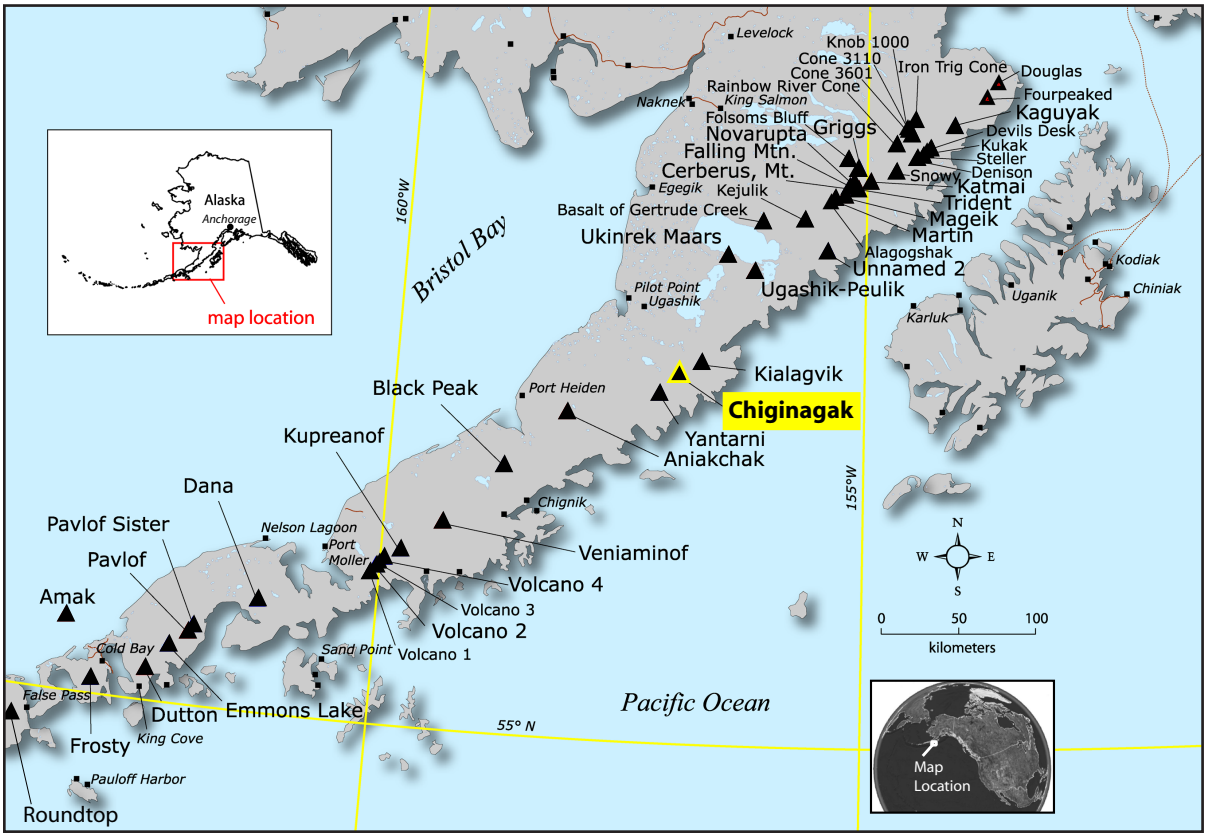

Figure 1. Location of Chiginagak volcano and nearby volcanoes on the Alaska Peninsula.

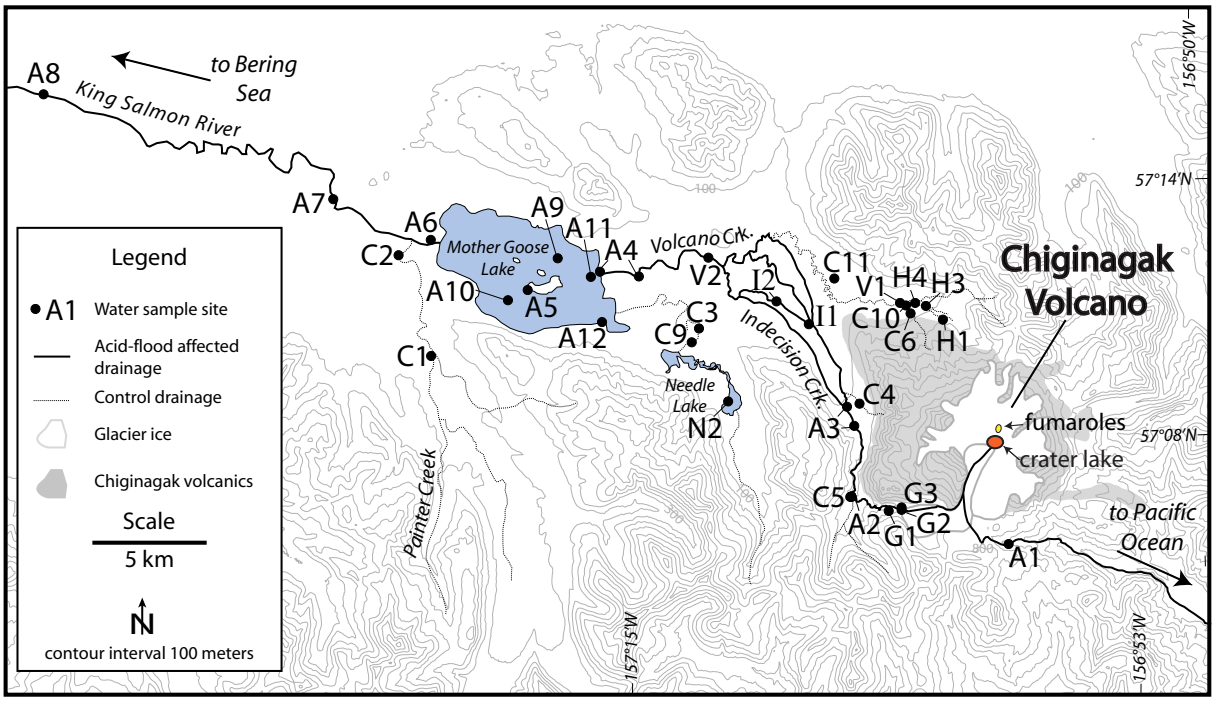

Figure 2. Map of water-sample locations and acid-flood-affected drainages around Chiginagak volcano.

Figure 3. Site A1 is a few hundred meters upstream of this photo and is the only water-sample site on the Pacific Ocean side of the field area. This stream drains into Chiginagak Bay. The red color along the stream bank is mainly from dead crowberry leaves that were damaged by the acidic aerosol cloud that accompanied the acid flood in May 2005 (Schaefer and others, 2008). Photo by J. Schaefer, August 20, 2005.

Figure 4. Site A2 in upper Indecision Creek is the acidic water stream that drains directly from the south flank glacier on Chiginagak volcano. The toe of the glacier is about 2.5 km upstream of this site. Site C5 is a clear-water, control tributary with headwaters in Naknek Formation sedimentary and igneous rocks (Detterman and others, 1987). The upper photo shows the red and orange color of the dead crowberry leaves that resulted from contact with the acidic aerosol cloud that accompanied the acid flood in May 2005, about 3½ months prior to the photo (Schaefer and others, 2008), and the lower photo from 2011 shows vegetation recovery since the acidic flood. Photos by J. Schaefer, August 20, 2005 (upper), and August 23, 2011 (lower).

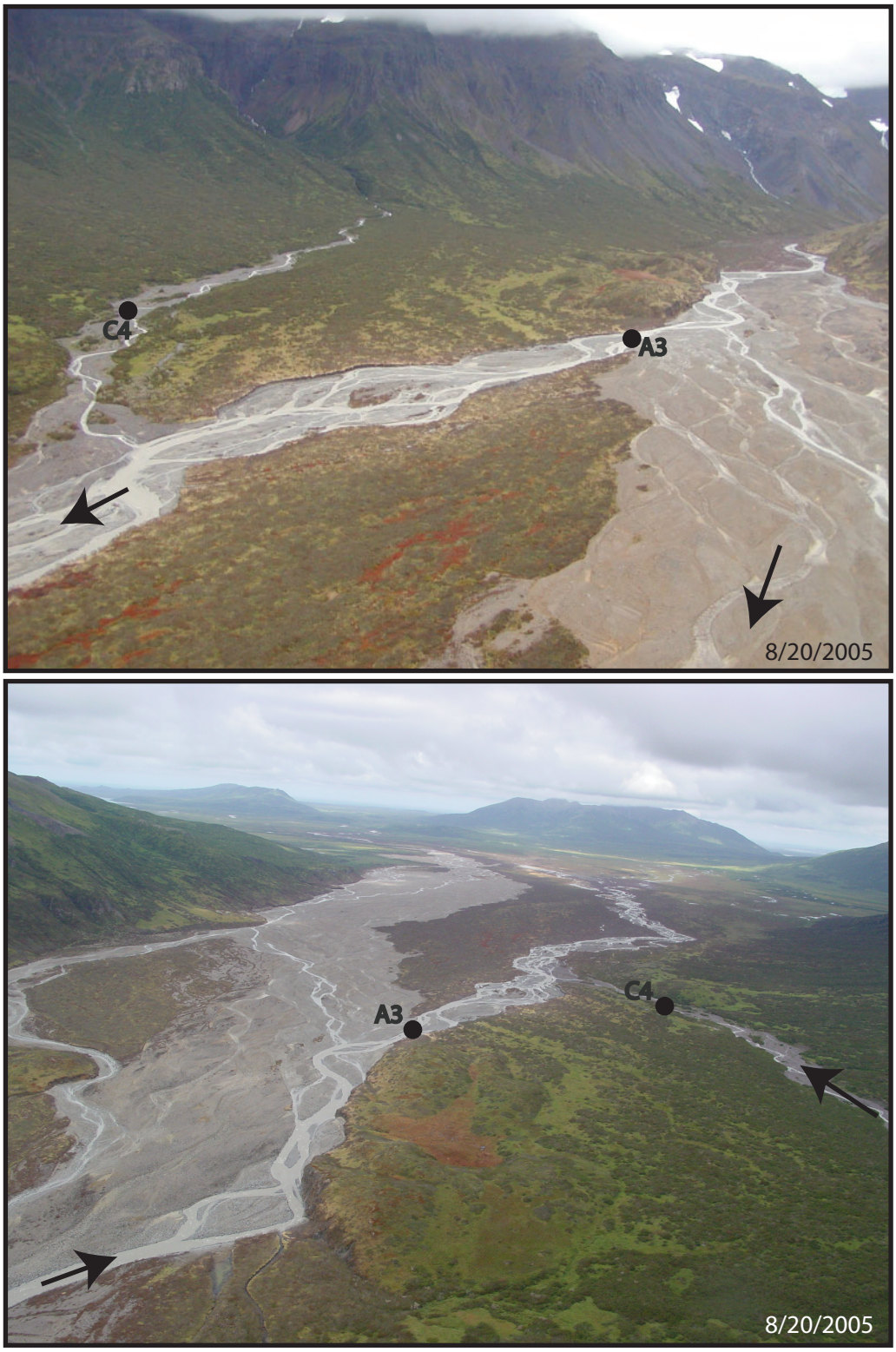

Figure 5. Site A3 in acid-water-affected mid Indecision Creek, and site C4, a control site on a tributary draining from the west side of Chiginagak volcano. The upper photo is looking upstream, and the lower photo is looking downstream, ~3½ months after the acid flood. Photos by J. Schaefer, August 20, 2005.

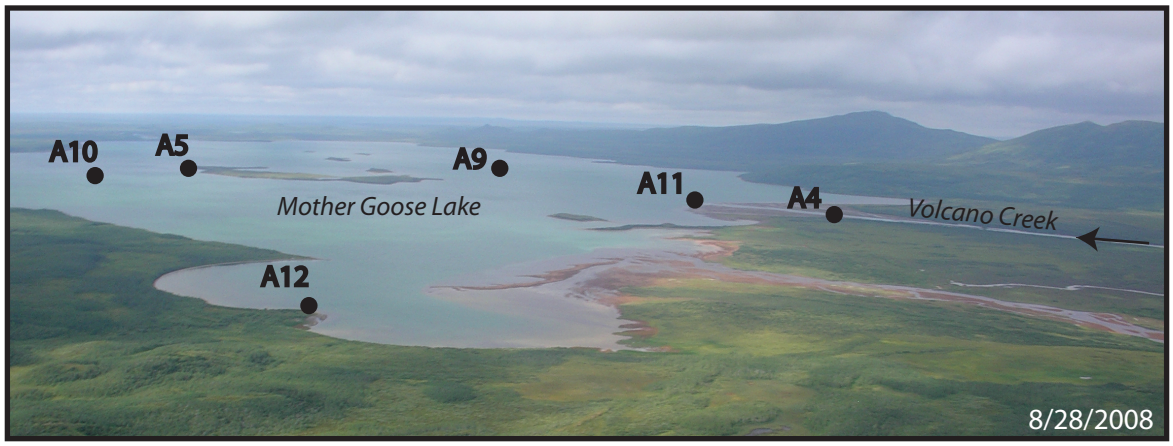

Figure 6. View to the north across Mother Goose Lake. Sites A9, A10, and A11 are in Mother Goose Lake and are accessible only by boat. Site A4 is at the mouth of Volcano Creek, site A5 is offshore of the largest island in the lake, and site A12 is along the lake shore near the USFWS cabin. During the course of fieldwork from 2005 to 2011, acidic water from the crater was flowing down upper Indecision Creek, across the valley in a northerly direction, then flowing into Volcano Creek at the north side of the valley, eventually making its way into Mother Goose Lake (fig. 2 and sites A4 and A11). The stream south of Volcano Creek in the foreground of this picture drains Needle Lake and a small, seasonal, western channel of Indecision Creek. Photo by J. Schaefer, August 28, 2008.

Figure 7. Game McGimsey (USGS) and Willie Scott (USGS) prepare to collect a water sample at site A4 at the mouth of Volcano Creek, about 200 m from the outlet to Mother Goose Lake. Photo by J. Schaefer, August 27, 2005.

Figure 8. Site A5 is a few meters offshore along the southwestern shore of the largest island in Mother Goose Lake. Photo by J. Schaefer, August 23, 2011.

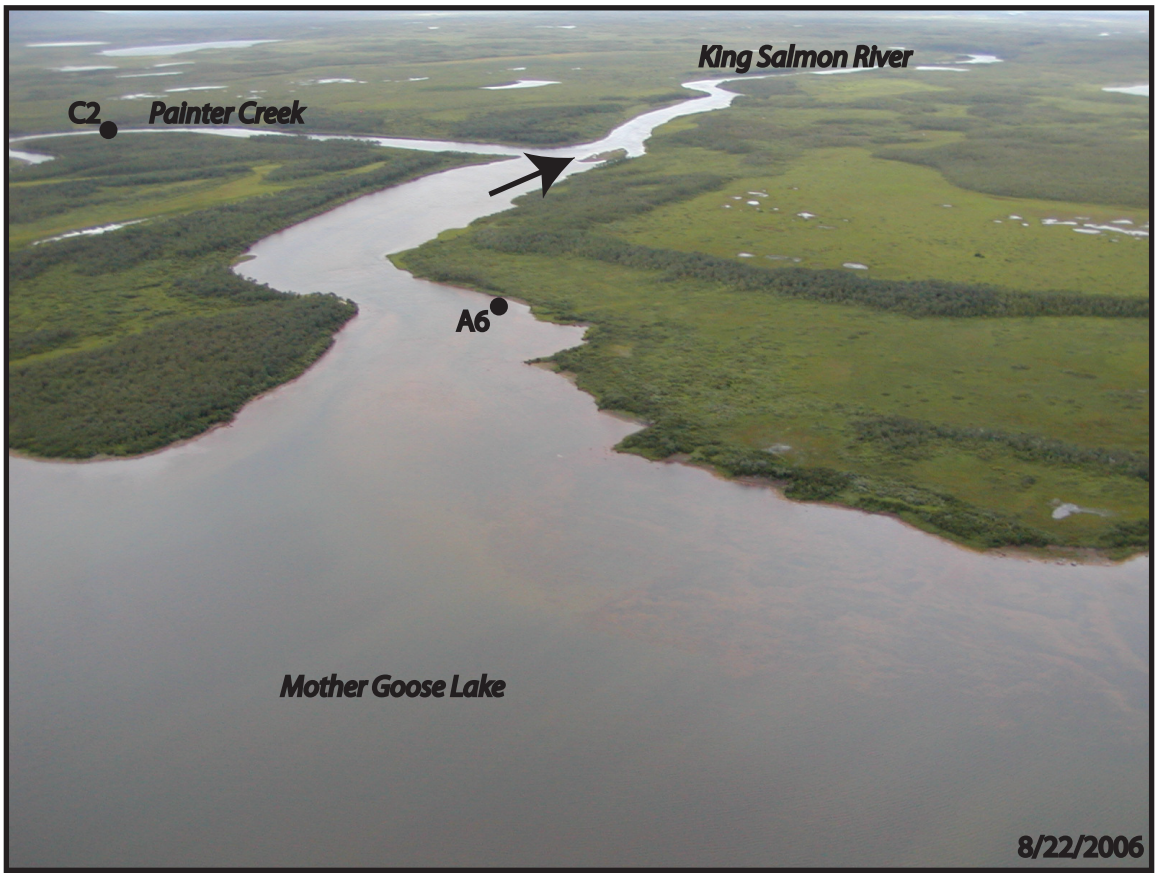

Figure 9. View to the west showing Site A6 at Mother Goose Lake outlet, and Site C2, a control site on lower Painter Creek. Note the orange colloidal iron oxides precipitated along the shore and bottom of the lake and river. Photo by J. Schaefer, August 22, 2006.

Figure 10. Game McGimsey (USGS) prepares to measure the pH at Site A6 along the shore of the King Salmon River at the outlet on the west end of Mother Goose Lake. The red structure is a privately owned cabin along the river. Photo by J. Schaefer, August 22, 2006.

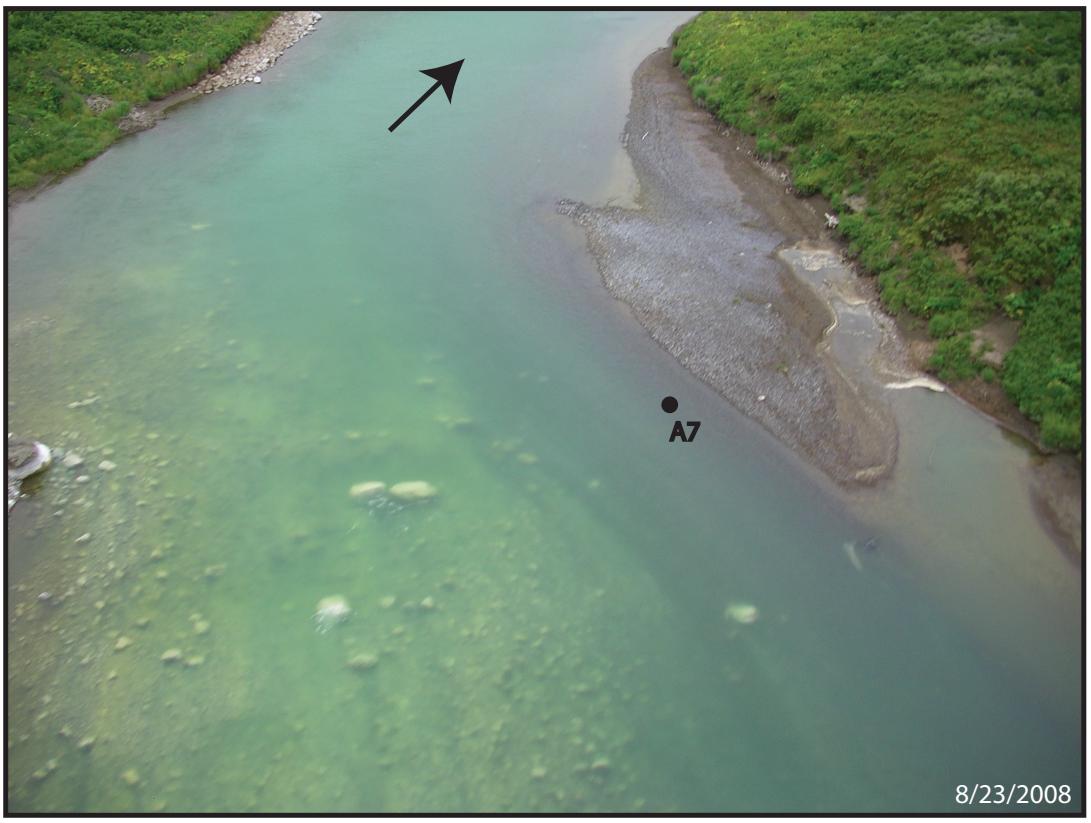

Figure 11. Site A7 on the upper King Salmon River about 4.3 km from the Mother Goose Lake outlet. Photo by W. Scott, August 23, 2008.

Figure 12. Site A8 on the lower King Salmon River about 18 km from the Mother Goose Lake outlet. Photo by J. Schaefer, August 23, 2005.

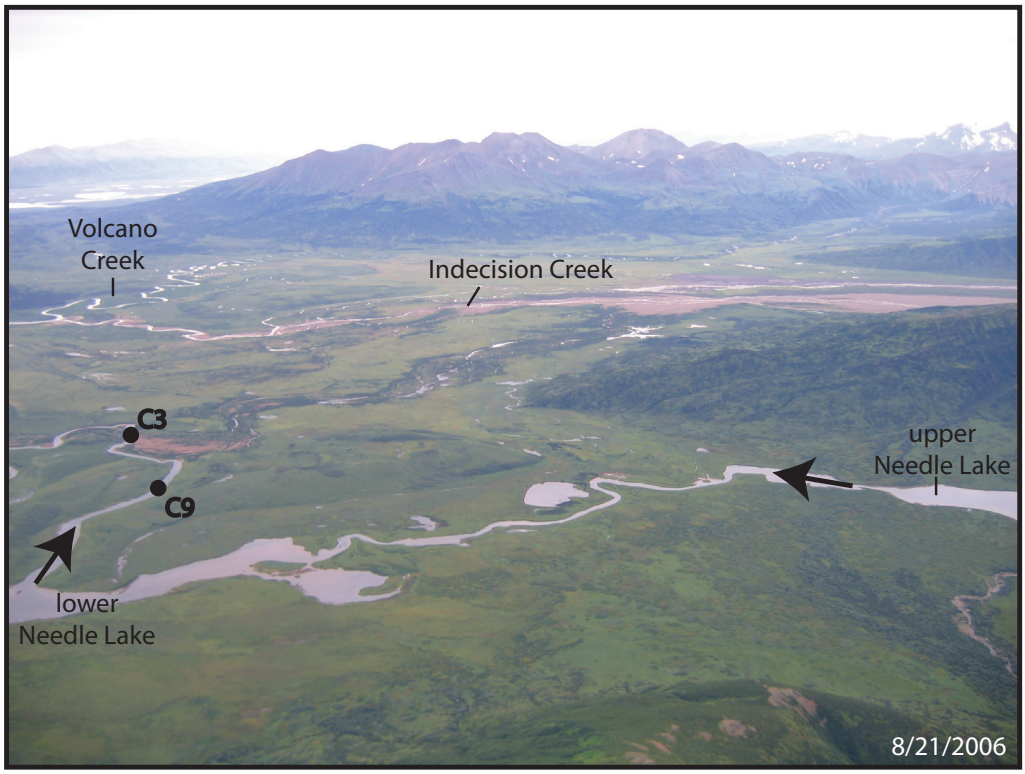

Figure 13. Control site C9 just downstream of lower Needle Lake outlet, and control site C3 lower in the valley. Photo by J. Jorgenson, August 21, 2006.

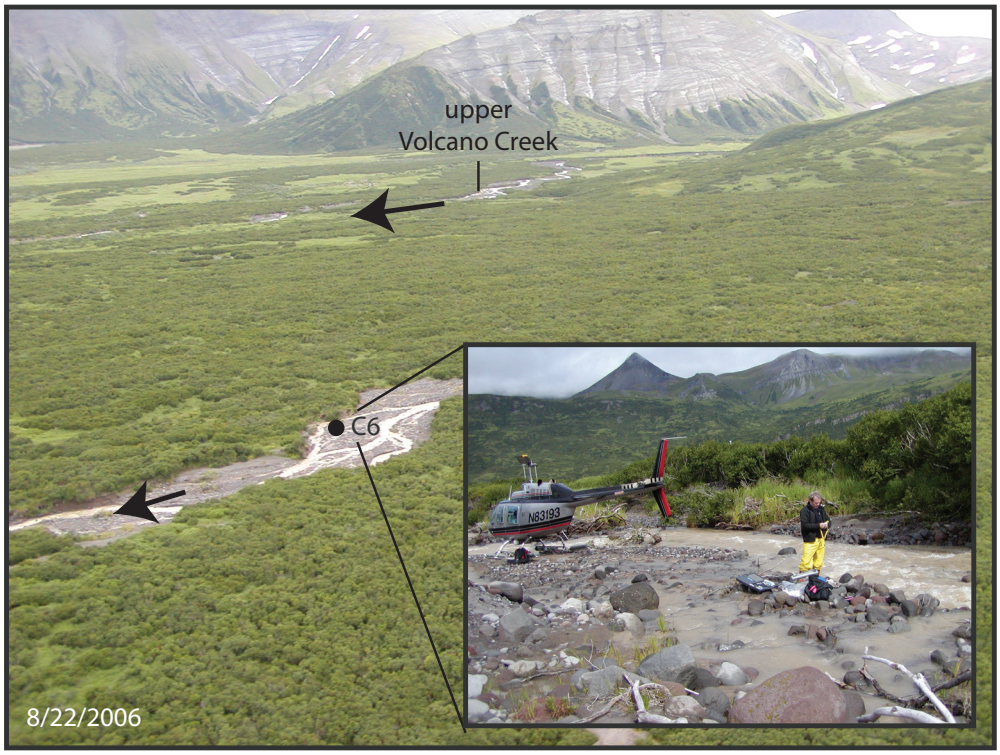

Figure 14. Site C6 is along a sediment-laden tributary to Volcano Creek, originating on the north flank of Chiginagak volcano. Site C10 is located farther downstream where this creek flows into Volcano Creek, seen in the background. Inset picture shows Game McGimsey (USGS) preparing to collect a water sample. Photos by J. Schaefer, August 22, 2006.

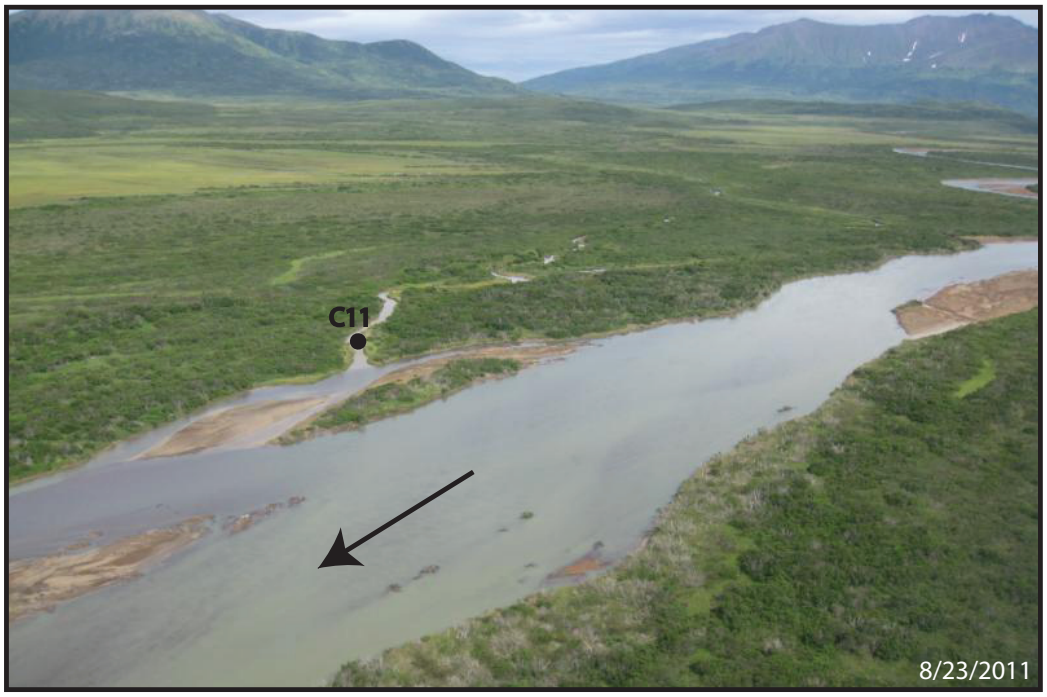

Figure 15. Site C11, near the mouth of a northern tributary to Volcano Creek (foreground). Photo by J. Schaefer, August 23, 2011.

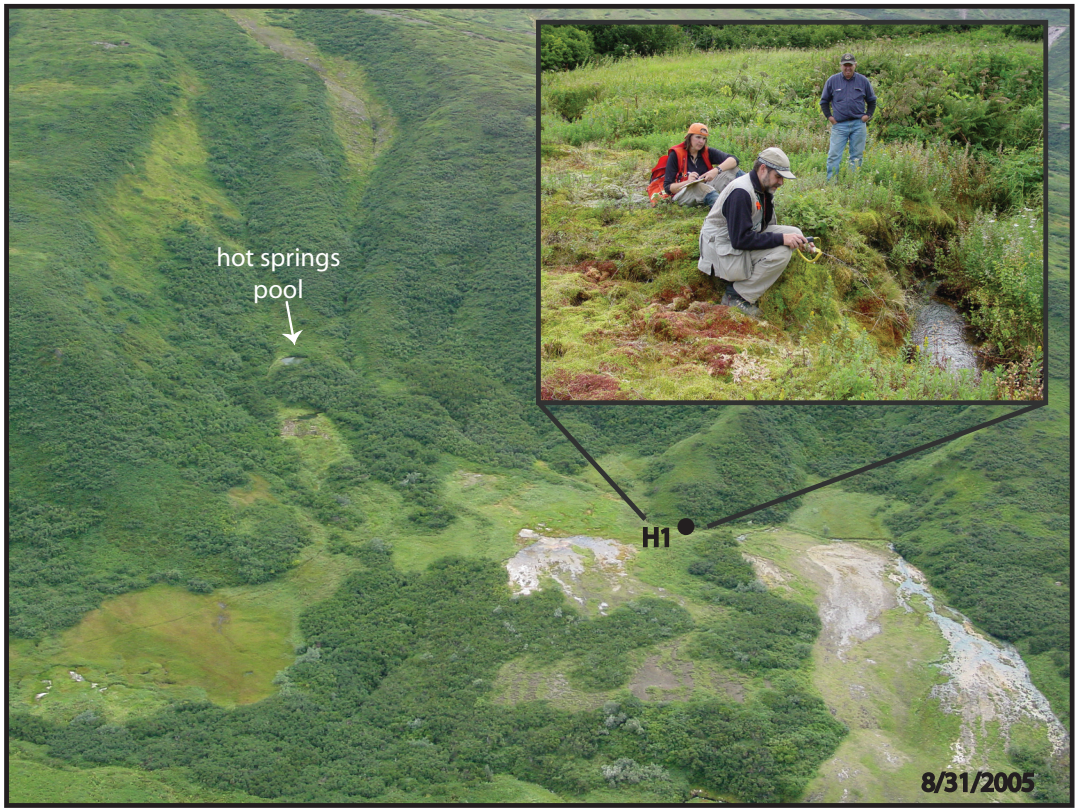

Figure 16. Mother Goose hot springs, site H1, located just above the valley floor along upper Volcano Creek. The sample site is downstream of the main hot-springs pool that sits perched in an alder patch higher up on the hillside. The inset photo shows a closer view of the hot-springs creek that drains the pool, with Janet Schaefer (DGGS) and Willie Scott (USGS) collecting water data; helicopter pilot in background. Photo by R.G. McGimsey, August 31, 2005.

Figure 17. Mother Goose hot springs, sites H1, H3, and H4, and Volcano Creek site V1. Photo by J. Schaefer, August 23, 2011.

Figure 18. Site V2 along Volcano Creek, just below the poplar grove, about 4.8 km upstream of where Volcano Creek enters Mother Goose Lake. Photo by J. Schaefer, August 23, 2011.

Table 1. Location of water samples near Chiginagak volcano.

Map Label	Longitude (wgs84)	Latitude (wgs84)	Location Description
A1	-156.9775	57.0916	Upper Chiginagak Creek; drains to the Pacific
A2	-157.0901	57.1120	Upper Indecision Creek
A3	-157.0908	57.1465	Mid Indecision Creek
A4	-157.2394	57.2007	About 200 m from the mouth of Volcano Creek near Mother Goose Lake
A5	-157.3214	57.1967	Mother Goose island; along the southwestern shore of the largest island in Mother Goose Lake
A6	-157.3954	57.2168	Mother Goose Lake outlet to King Salmon River, across from private cabin
A7	-157.4614	57.2320	Upper King Salmon River; below Painter Creek
A8	-157.6675	57.2774	Lower King Salmon River
A9	-157.2933	57.2089	Northern deep basin of Mother Goose Lake
A10	-157.3350	57.1961	Southern deep basin of Mother Goose Lake
A11	-157.2756	57.2023	Volcano Creek inlet to Mother Goose Lake; station in the lake
A12	-157.2661	57.1837	Along the shore of Mother Goose Lake near the USFWS cabin
C1	-157.3954	57.1809	Mid Painter Creek
C2	-157.4131	57.2114	Lower Painter Creek
C3	-157.1969	57.1797	Needle Lake outflow
C4	-157.0833	57.1491	Clear-water tributary to Mid Indecision Creek
C5	-157.0908	57.1119	Clear-water tributary to Upper Indecision Creek
C6	-157.0435	57.1838	Tributary to upper Volcano Creek
C9	-157.2017	57.1746	Needle Lake outflow, upstream of C3
C10	-157.0465	57.1874	Tributary to Volcano Creek that drains small north side glaciers of Chiginagak volcano
C11	-157.1006	57.1967	Small tributary to Volcano Creek
G1	-157.0559	57.1059	Toe of southern flank glacier; 1st stream from south
G2	-157.0479	57.1048	Toe of southern flank glacier; 2nd stream from south
G3	-157.0488	57.1058	Toe of southern flank glacier; 3rd stream from south
H1	-157.0203	57.1805	Mother Goose MG1 hot spring
H3	-157.0214	57.1811	Lower hot-springs creek
H4	-157.0232	57.1819	Hot-springs inflow to Volcano Creek
I1	-157.1142	57.1767	Lower Indecision Creek
I2	-157.1406	57.1891	Lower Indecision Creek; downstream of I1
N2	-157.1791	57.1501	Upper Needle Lake
V1	-157.0465	57.1874	Upper Volcano Creek
V2	-157.1887	57.2076	Mid Volcano Creek

SURFACE-WATER pH

The acidity of Mother Goose Lake has decreased (pH increase) since the first measurements were taken in 2005, 3½ months after the acid-flood event [table 2 (*Table_2_Chiginagak_water_chemistry_pH_2005-2012.xlsx)* and fig. 19]. The pH of Mother Goose Lake increased from the lowest measured pH of 2.9 in September 2005 to a high of 6.9 in August 2011 (site A5).

In August and September 2010, DGGS conducted fieldwork with U.S. Fish & Wildlife Service (USFWS) fisheries biologists, sampling water and investigating the recovery of fish in the acidified system. Biologists found that a variety of fish species had returned to Mother Goose Lake in 2010, and a pH measurement of 5.2 at site A5 confirmed that the acidity of the lake had declined (Scott Ayers, USFWS, written commun.). Of note is the return of fish to Mother Goose Lake corresponding to the rise in pH above 5, the pH at which Al becomes insoluble. Toxic forms of Al are relatively insoluble at neutral to alkaline pH, but at pH less than 5, the toxic species Al^{3+} becomes soluble (Delhaize and Ryan, 1995). In addition to Al, high levels of Fe in the acidic water likely contributed to toxic conditions for the fish (Vuori, 1995).

SURFACE-WATER CHEMISTRY

Since 2005, Chiginagak water samples have been analyzed for both anion and cation concentrations at USGS water-chemistry labs (methods described in Schaefer and others, 2008; results in attached digital file *Table_2_Chiginagak_water_chemistry_pH_2005-2012.xlsx*). In 2011, additional water samples were collected and submitted for analysis; results are now included as an addendum to version 2 of this report. Limited water sampling took place prior to this study: Baker and others (1977) provide water-chemistry data for Needle Lake, Volcano Creek, and Mother Goose hot springs, and Motyka and others (1981) also report water-chemistry data for Mother Goose hot springs.

U.S. Environmental Protection Agency (EPA) priority pollutant levels have been evaluated in all samples collected. In 2005, approximately 3 months after the crater lake flood, only Cd and Cu exceeded the chronic exposure standards in Mother Goose Lake. These concentrations have now declined (fig. 20). We expect this trend to continue as acidic water input from the crater lake decreases.

CRATER LAKE OBSERVATIONS

Photographs of the summit crater between 2004 and 2011 (excluding 2007) provide a striking record of changing conditions (figs. 21–28). In 2004, about one year prior to the melting and flood event, the summit of Chiginagak crater was filled with ice and snow (figs. 21 and 28). The next photographs of the summit were taken in August 2005, about 3½ months after the flood event, and show a ~300-m-wide crater lake with a small zone of upwelling (~10 m wide) near the lake center (figs. 22 and 28). The upwelling is inferred to represent the ascent of hot gas and water from a submerged fumarolic source on the crater floor.

Annual photographs after 2005 show a steady decline in lake level as water continued to drain, likely through

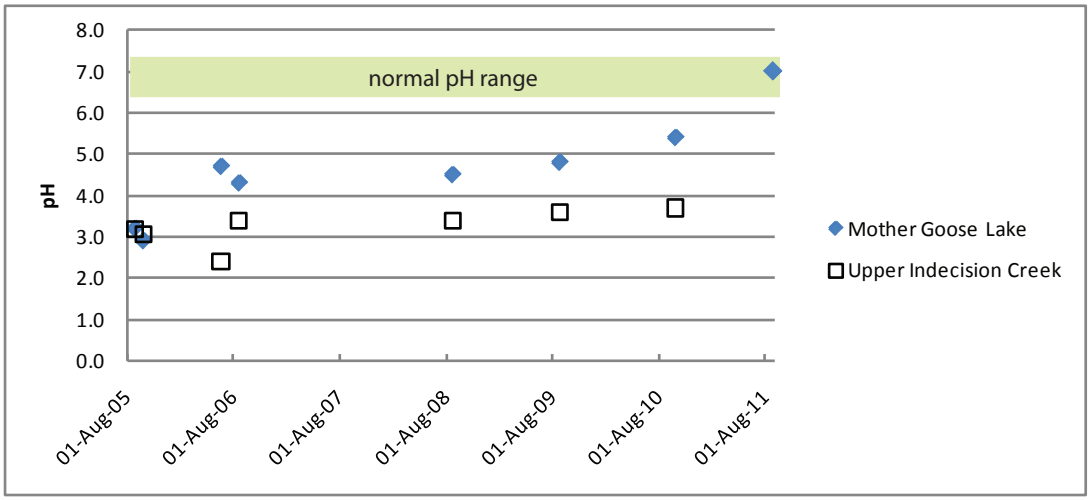

Figure 19. Surface water pH levels from August 2005 through August 2010 in Mother Goose Lake and Indecision Creek. Normal pH in control waters ranges from about 6.5 to 7.3.

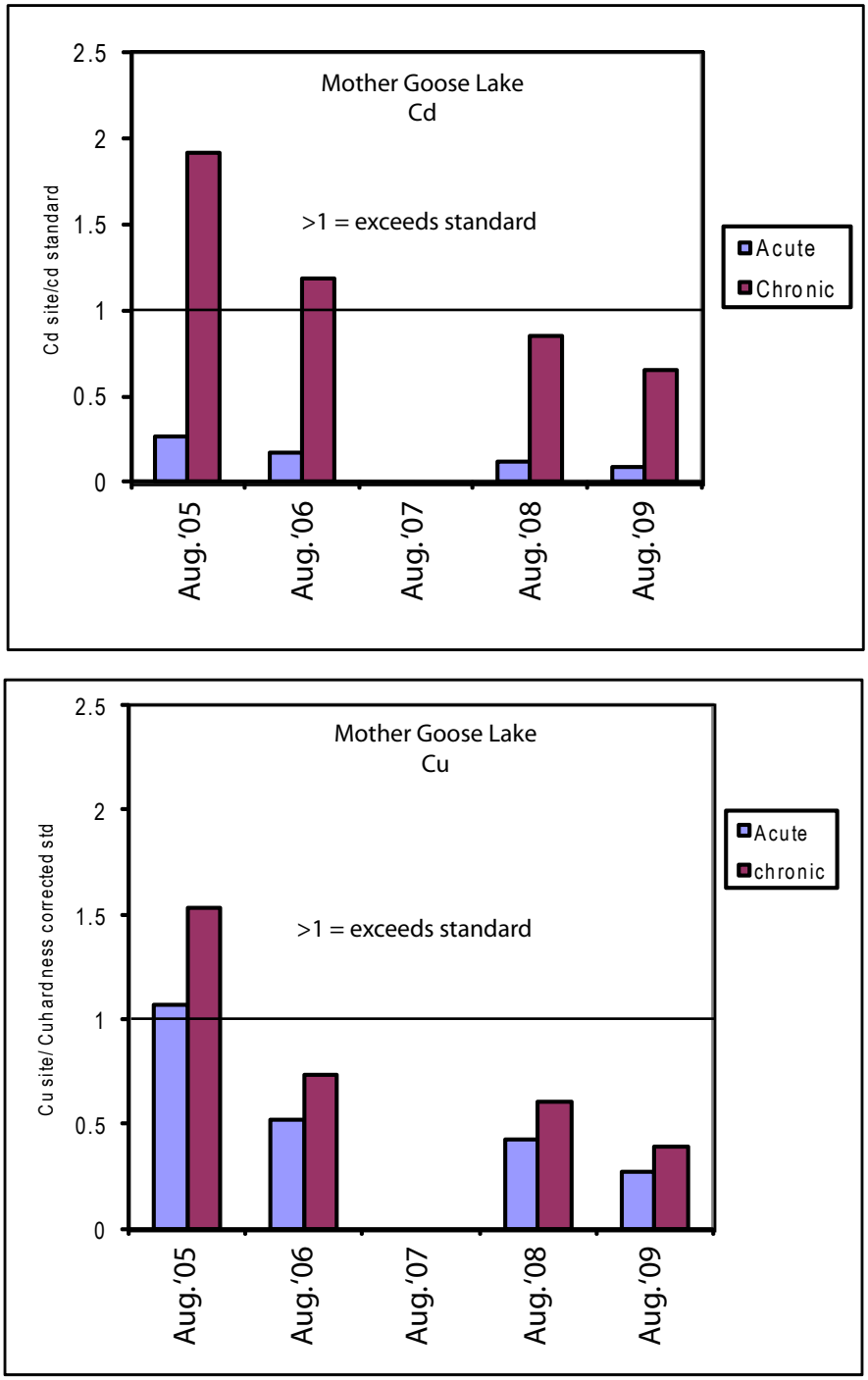

Figure 20. Histograms showing August 2005 through August 2009 concentrations of the priority pollutants Cd and Cu in Mother Goose Lake relative to 2007 U.S. EPA chronic and acute exposure standards. Note: Acute and chronic exposure standards for Cu were calculated with a hardness correction model using Mg and Ca. The biotic ligand model was not used because dissolved organic carbon values are unknown.

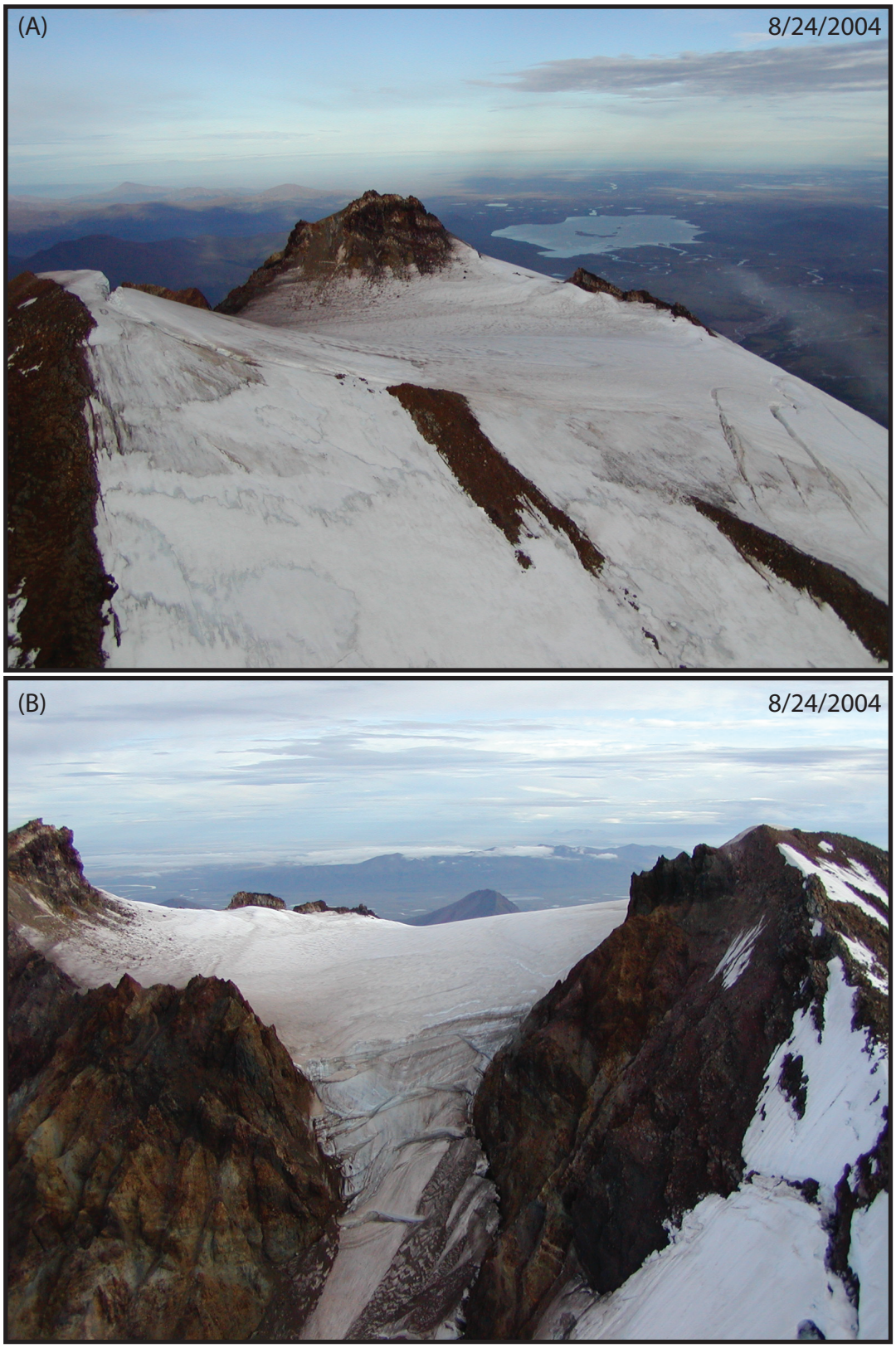

Figure 21. The snow- and ice-filled summit crater of Chiginagak volcano on August 24, 2004, prior to the acid flood event: (A) View east with Mother Goose Lake in the background, and (B) South crater rim showing the head of the south flank glacier. Photos by J. Schaefer, August 24, 2004.

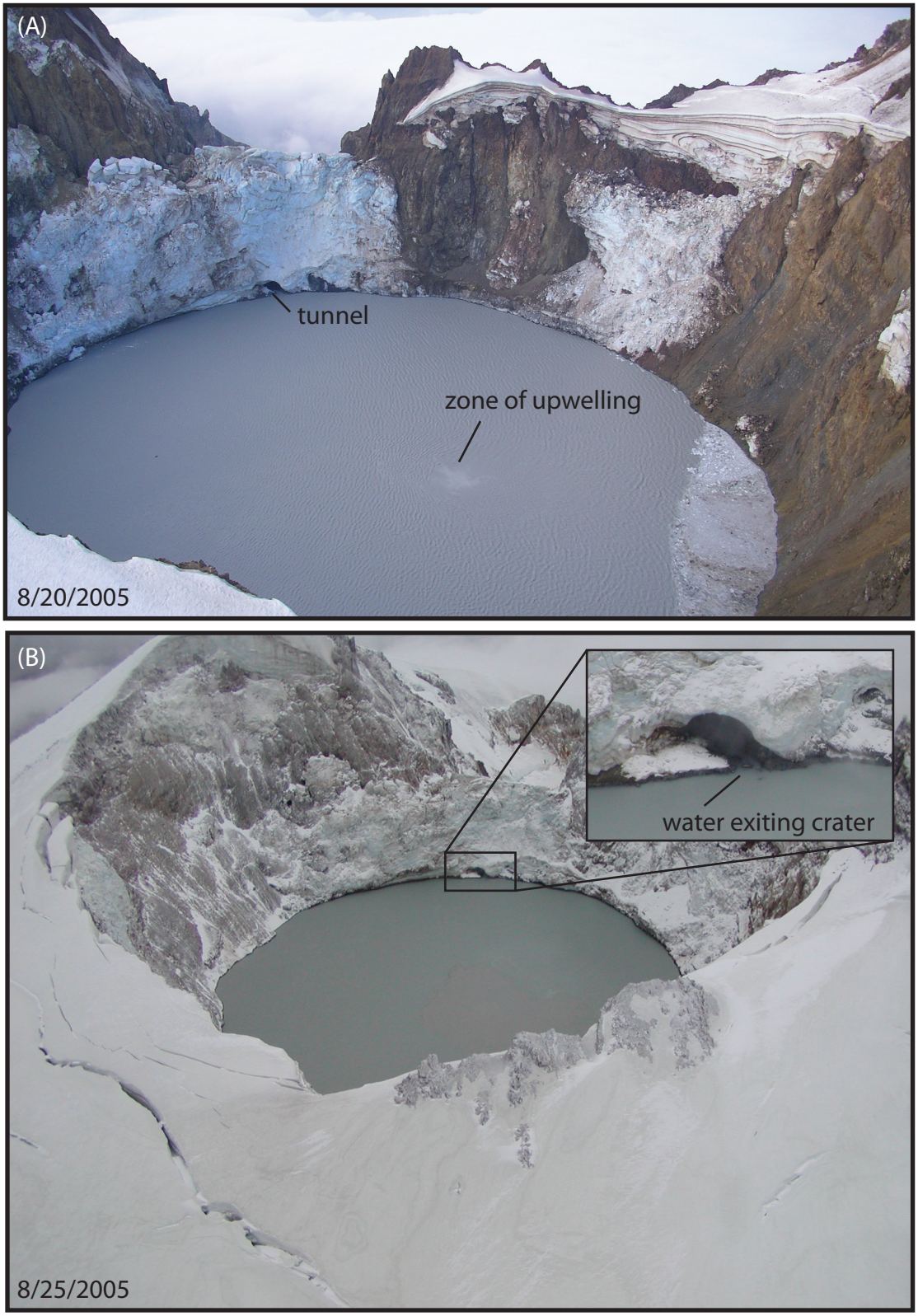

Figure 22. Chiginagak crater lake ~3½ months after the flood event on (A) August 20, 2005, and (B) August 25, 2005, showing water exiting the crater through a tunnel at the ice–rock interface along the south crater rim, and the zone of upwelling just off-center in the crater lake. Photos by J. Schaefer.

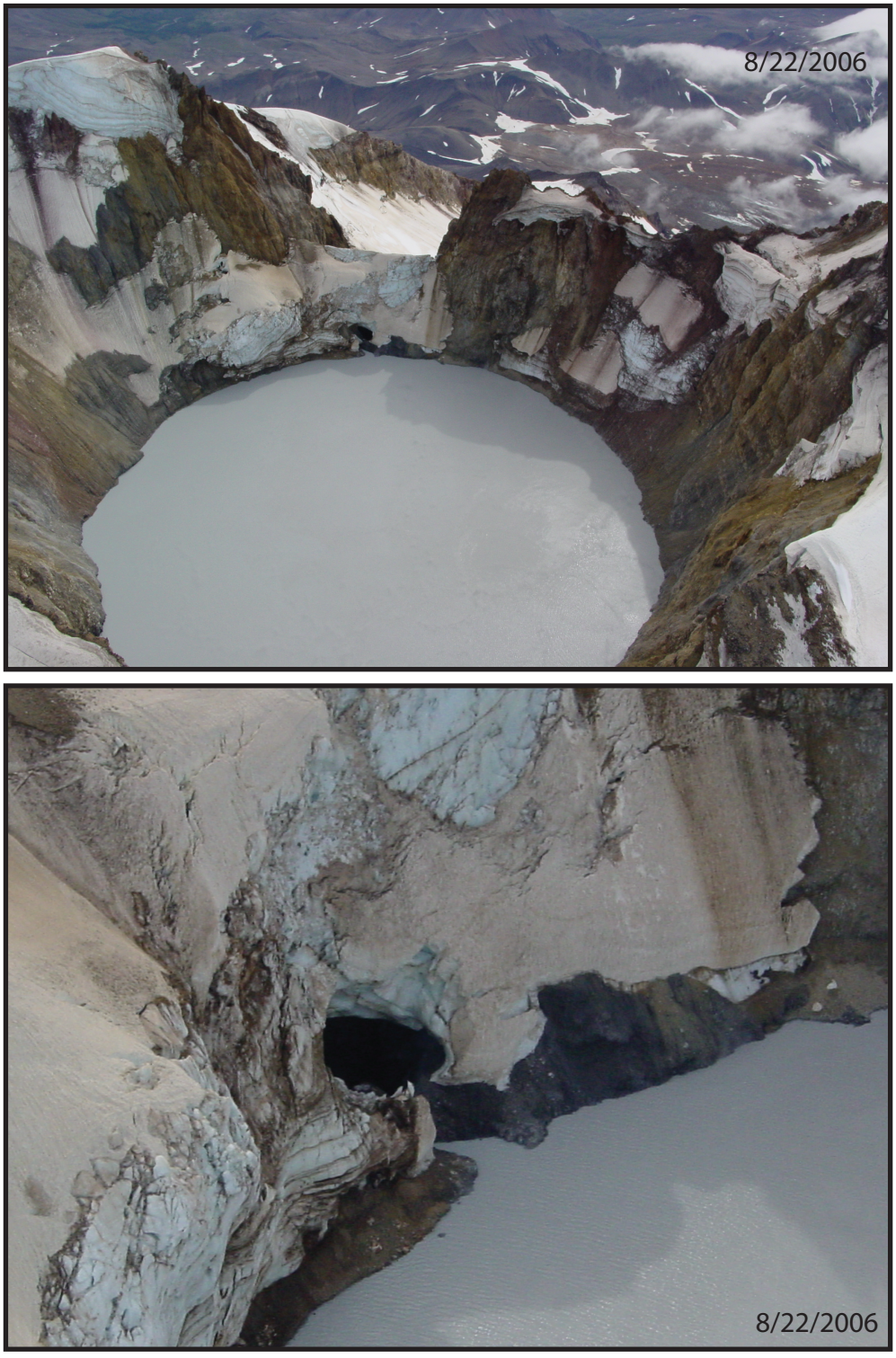

Figure 23. Chiginagak crater lake on August 22, 2006. The lake level has dropped ~6–7 m from previous observations in August 2005 (fig. 22). The lower photo shows a deepened and eroded channel where water enters the tunnel beneath the glacier. Photos by J. Schaefer, August 22, 2006.

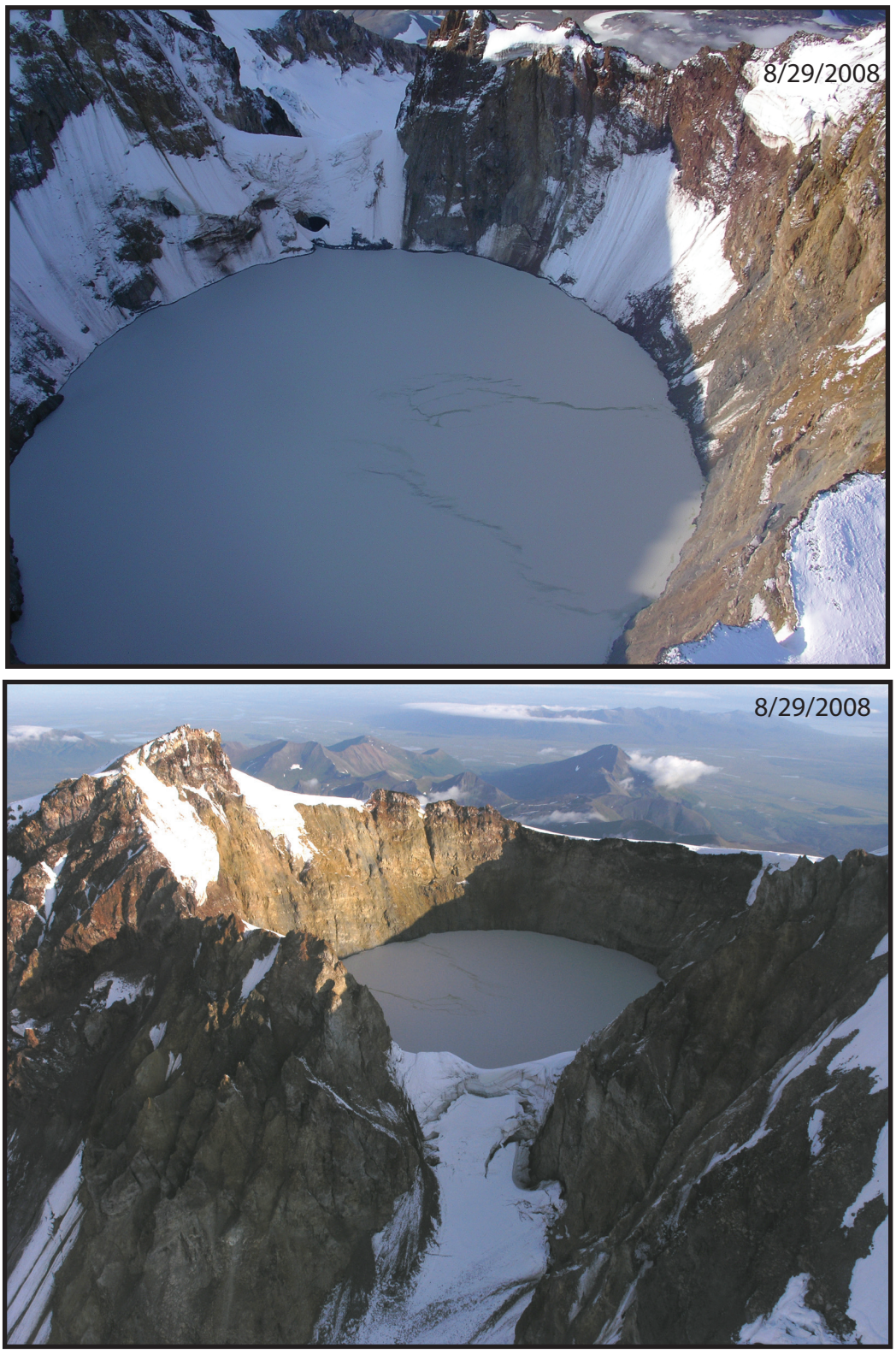

Figure 24. Chiginagak crater lake on August 29, 2008. The lake level appears unchanged from August 2006 observations. No observations or photographs of the lake were made in 2007. Upper image is a view to the south, lower image is a view to the north. Photos by J. Schaefer, August 29, 2008.

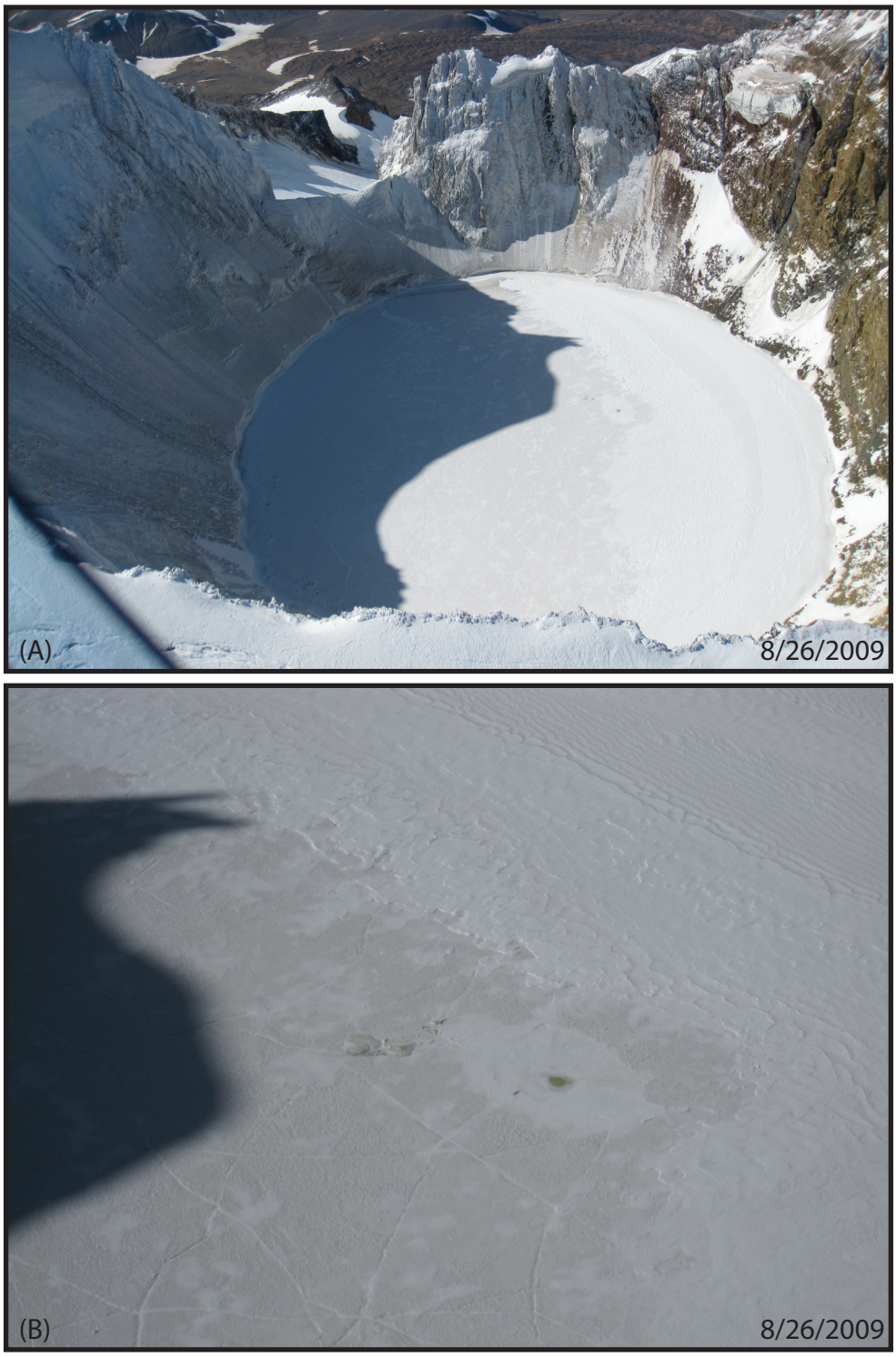

Figure 25. Chiginagak crater lake on August 26, 2009. Ice covers the lake, and the location of previous upwelling is marked by a small circular patch of yellow sulfur in the ice: to the right of center in top image (A) and closer view in lower image (B). Photos by J. Schaefer.

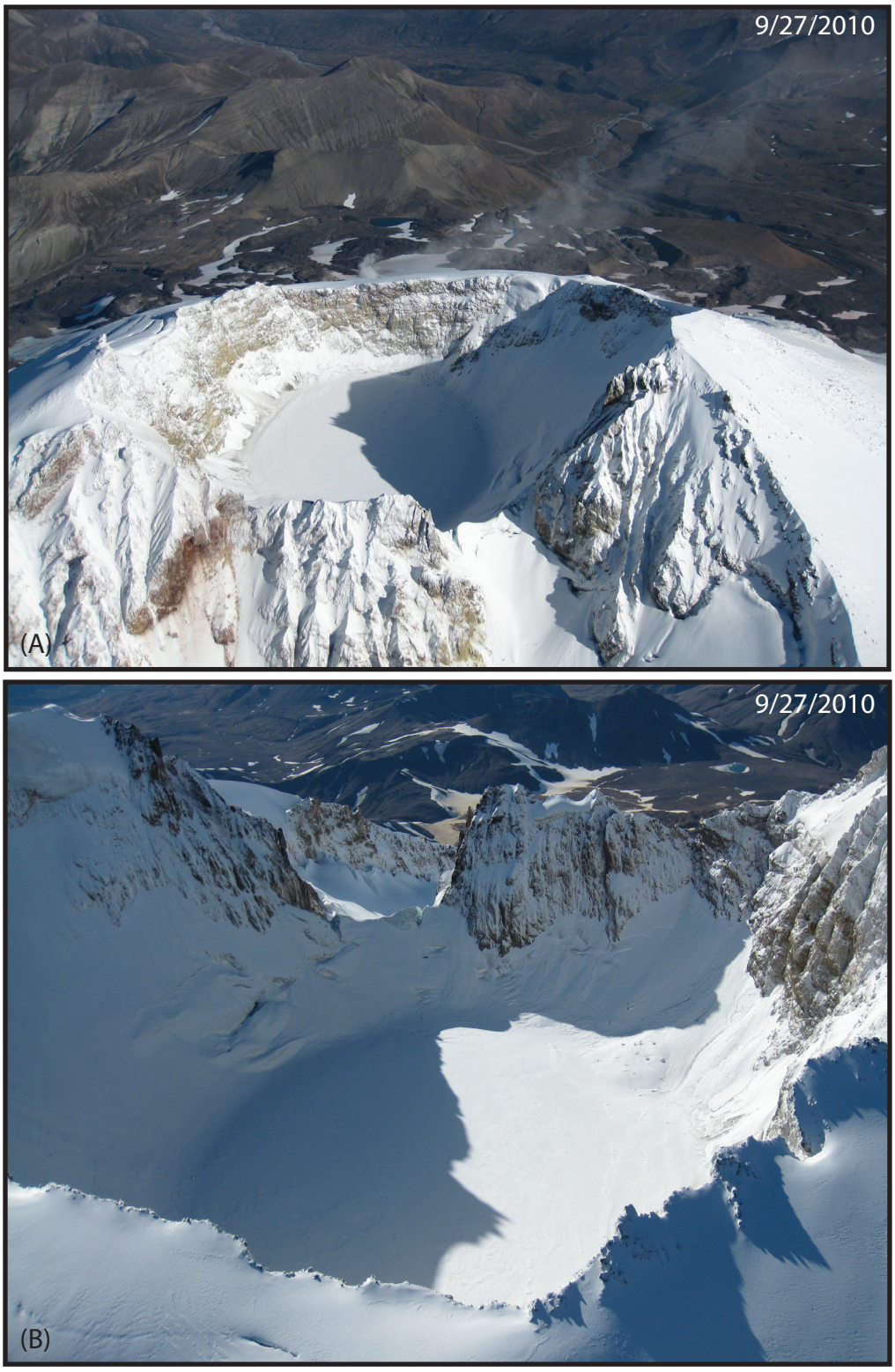

Figure 26. Chiginagak crater lake on September 27, 2010. The lake surface is covered with snow and ice and the drainage tunnel through the ice is no longer visible. (A) View to the northeast, and (B) view to the south. Photos by J. Schaefer.

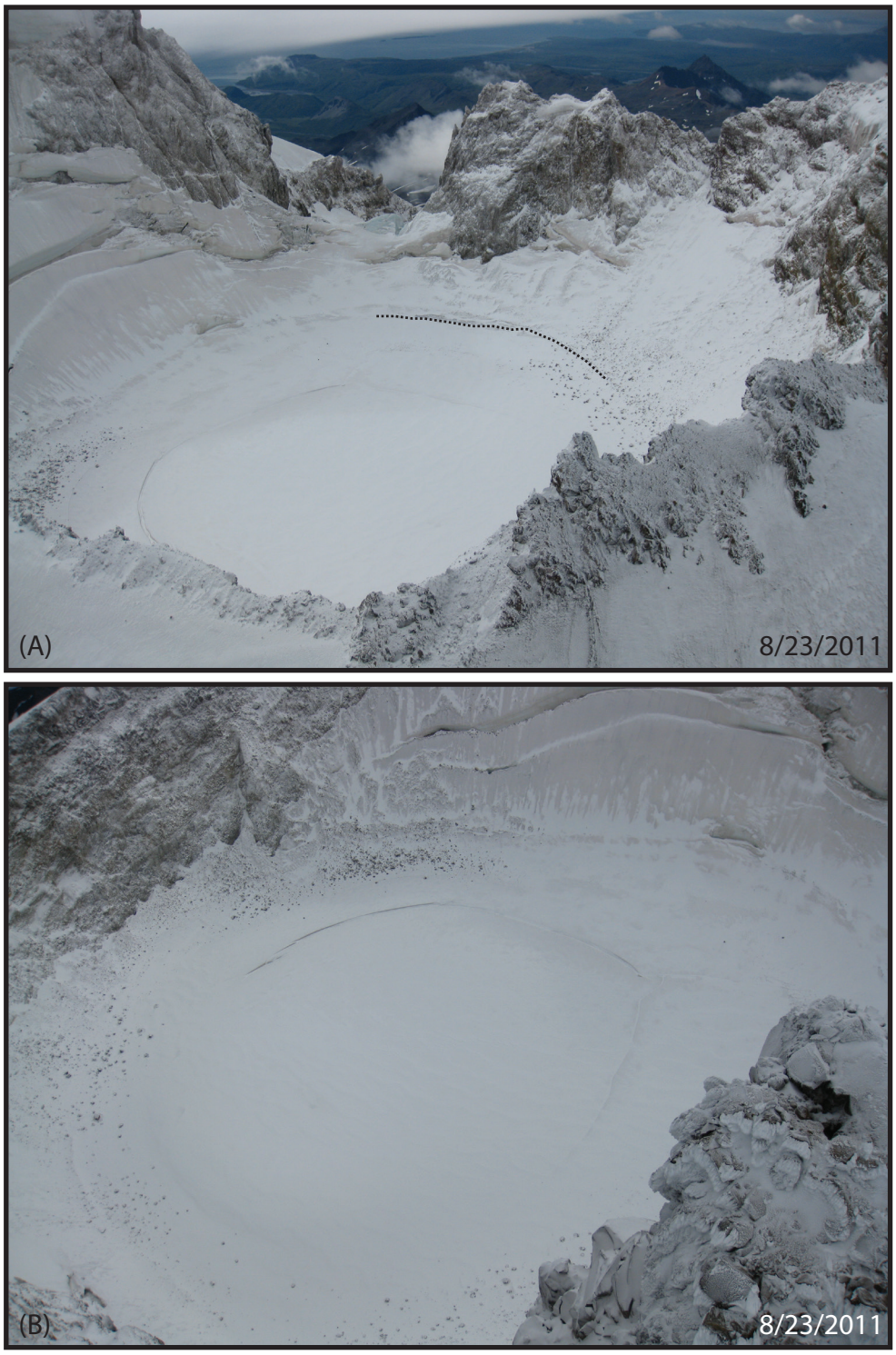

Figure 27. Chiginagak summit crater on August 23, 2011. (A) The level of the ice-covered lake dropped ~50 m between September 2010 and August 2011 and is well below the former outlet tunnel. The dashed line shows the post-flood 2005 lake level. The left edge of the dashed line ends at the approximate location of the tunnel, now obscured by snow and ice. (B) View to the east. Photos by J. Schaefer.

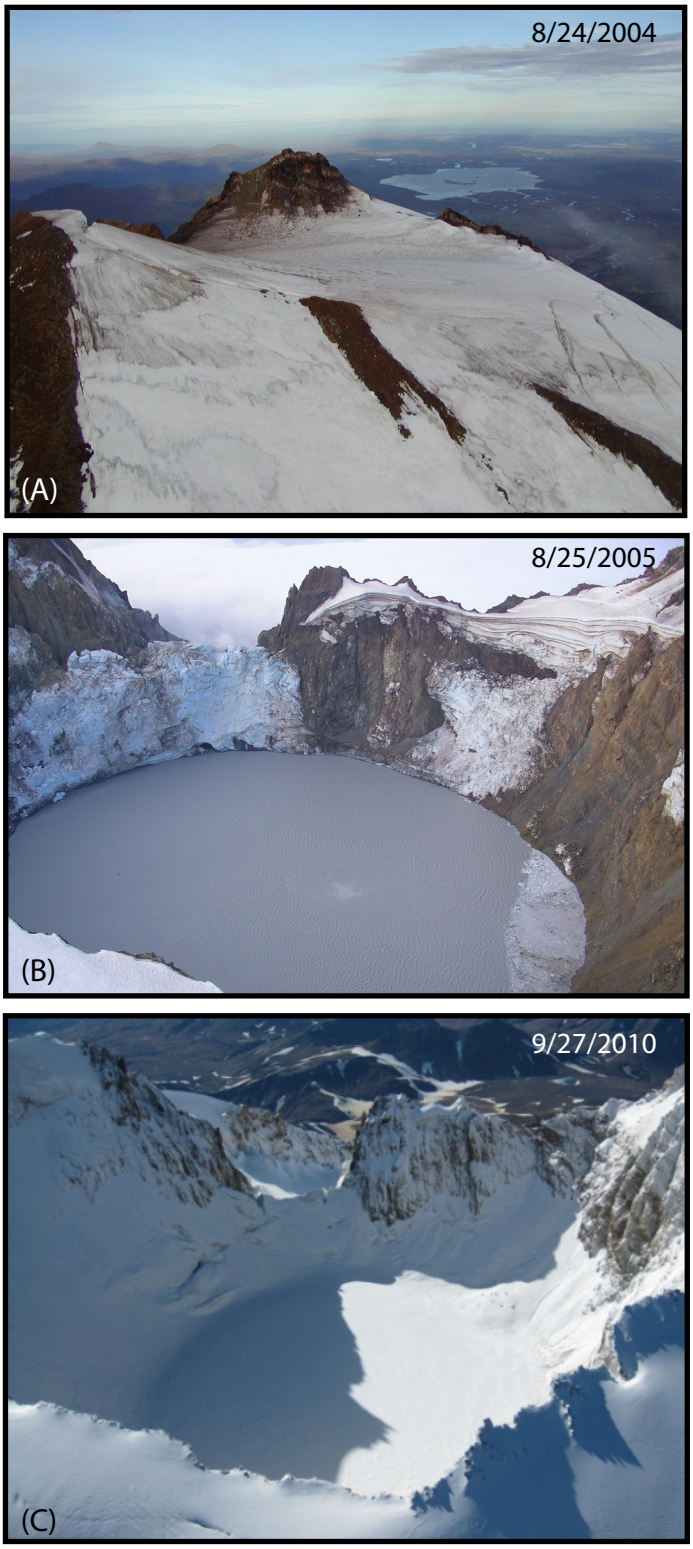

Figure 28. Crater lake images showing the change from 2004 through 2010. (A) A pre-flood ice-filled crater in August 2004 (Mother Goose Lake in background), to (B) a partially drained crater lake in August 2005, 3½ months after the flood, and (C) the accumulation of snow and ice in September 2010. Photos by J. Schaefer.

joints and cracks in the altered rocks of the summit region, eventually draining out beneath the south flank glacier into upper Indecision Creek. Beginning in 2009, four years after the flood, the surface of the crater lake began to freeze, indicating a marked reduction in the crater's fumarolic heat. In 2010 we observed additional accumulation of snow and ice in the crater and a slight drop in lake level (figs. 26 and 28). Despite the newly frozen lake surface, liquid water beneath the ice in the crater continued to drain and supply acidic water to Indecision Creek, Mother Goose Lake, and the King Salmon River. Between September 2010 and August 2011, the crater lake level dropped by an additional ~50 m (fig. 27).

Figure 29. Images of the Chiginagak volcano north flank fumaroles from 1994 through 2011. (A) May 9, 1994, photo by C. Nye, (B) September 28, 1998, photo by D. Schneider, (C) August 24, 2004, photo by W. Scott, (D) August 27, 2005, photo by R.G. McGimsey, (E) June 21, 2006, photo by C. Read, (F) June 21, 2006, photo by C. Read, (G) November 24, 2008, photo by R. Dreeszen, (H) August 26, 2009, photo by J. Schaefer, (I) September 27, 2010, photo by J. Schaefer, (J) August 23, 2011, photo by J. Schaefer.

SUMMARY AND OUTLOOK

The draining and freezing of acidic water in the summit crater, and the increasing pH of Indecision Creek, indicate that the increase in heat flux that manifested in 2005 has ended and the summit fumarolic activity has ceased. The long-lived fumaroles on the north flank (fig. 29) continue to emit steam and other volcanic gases much as they had before and during the 2005 event. Clearly the volcano's hydrothermal system remains active even though the source of the summit-crater heating has greatly diminished. Although the crater lake is freezing, some water likely remains under the ice, draining beneath the south flank glacier into Indecision Creek, continuing to supply acidic water to Mother Goose Lake. Despite this acid input, acidity in Mother Goose Lake is decreasing, fish are returning, and time-series trends show decreasing concentrations of priority pollutants. We expect these trends to continue as input of acidic water from the crater lake declines. Evidence of acid flood events in past decades indicates that such activity is a recurrent process at Chiginagak volcano (Schaefer and others, 2008; Kassel, 2009).

ACKNOWLEDGMENTS

This work was made possible with funding from the U.S. Geological Survey's Volcano Hazard Program as well as the U.S. Department of Interior, Fish and Wildlife Service (USFWS). Special thanks is due to Doug McBride of the USFWS Anchorage Field office, who took a special interest in this project and was instrumental in establishing the cooperative agreement between the State of Alaska Department of Natural Resources, Division of Geological & Geophysical Surveys, and the USFWS that funded much of the water sampling. We appreciate the assistance of the USFWS King Salmon field office personnel, especially Ron Britton. Thanks also to USFWS personnel Scott Ayers, Jon Gerken, and Theresa Tanner, who were extremely helpful in the field. We appreciate the constructive reviews by Christina Neal (U.S. Geological Survey) and Cheryl Cameron (Alaska Division of Geological & Geophysical Surveys).

REFERENCES

Baker, R.O., Lebida, R.C., Pyle, W.D., and Britch, R.P., 1977, An investigation of selected Alaska geothermal spring sources as possible salmon hatchery sites: National Technical Information Service IDO/1624-1, 173 p.

Coats, R.R., 1950, Volcanic activity in the Aleutian Arc: U.S. Geological Survey Bulletin B 0974-B, p. 35–49, 1 sheet, scale unknown.

Delhaize, E., and Ryan, P.R., 1995, Aluminum toxicity and tolerance in plants: Plant Physiology, v. 107, p. 315–321.

Detterman, R.L., Wilson, F.H., Yount, M.E., and Miller, T.P., 1987, Quaternary geologic map of the Ugashik, Bristol Bay, and western part of Karluk quadrangles, Alaska: U.S. Geological Survey Miscellaneous Investigations Series Map I-1801, unpaged, 1 sheet, scale 1:250,000.

Kassel, C.M., 2009, Lacustrine evidence from Mother Goose Lake of Holocene geothermal activity at Mount Chiginagak, Alaska Peninsula: Flagstaff, Arizona, Northern Arizona University, unpublished M.S. thesis, 138 p.

Motyka, R.J., Moorman, M.A., and Liss, S.A., 1981, Assessment of thermal spring sites, Aleutian arc, Atka Island to Becharof Lake—Preliminary results and evaluation: Alaska Division of Geological & Geophysical Surveys Alaska Open-File Report 144, 179 p.

Powers, H.A., 1958, Alaska Peninsula–Aleutian Islands, *in* Williams, H., ed., Landscapes of Alaska: Los Angeles, CA, University of California Press, p. 61–75.

Schaefer, J.R., Scott, W.E., Evans, W.C., Jorgenson, J., McGimsey, R.G., and Wang, B., 2008, The 2005 catastrophic acid crater lake drainage, lahar, and acidic aerosol formation at Mount Chiginagak volcano, Alaska, USA—Field observations and preliminary water and vegetation chemistry results: Geochemistry Geophysics Geosystems, v. 9, no. 7, 29 p., Q07018, doi:10.1029/2007GC001900.

Vuori, K., 1995, Direct and indirect effects of iron on river ecosystems, Annales Zoologici *Fennici, v. 32*, p. 317–329.