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Source: Arctic, Antarctic, and Alpine Research, 42(3) : 245-249

Published By: Institute of Arctic and Alpine Research (INSTAAR), University of Colorado

URL: <https://doi.org/10.1657/1938-4246-42.3.245>

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# Introduction—The Impacts of the 2008 Eruption of Kasatochi Volcano on Terrestrial and Marine Ecosystems in the Aleutian Islands, Alaska

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DOI: 10.1657/1938-4246-42.3.245

## Introduction

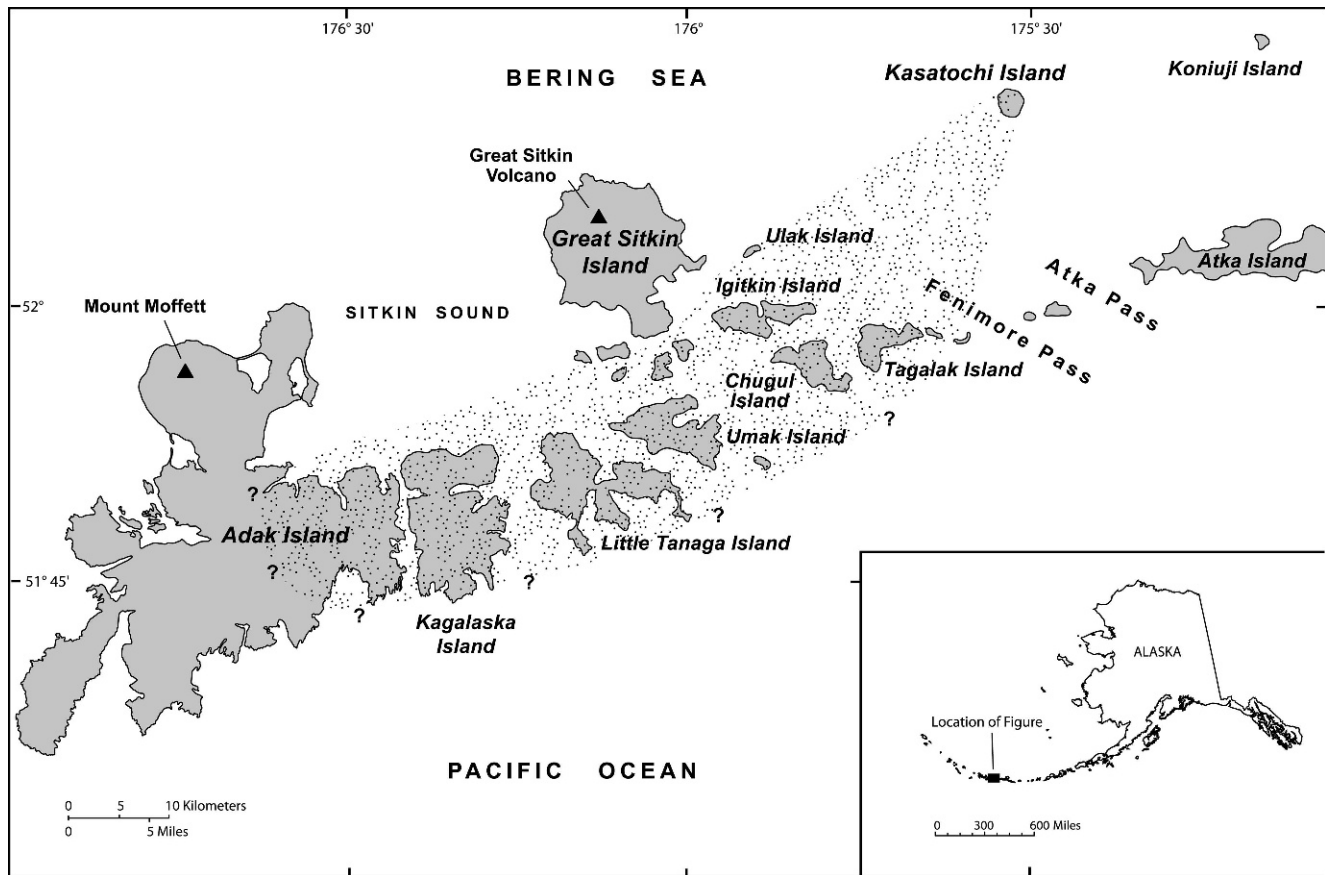
The Aleutian Islands are situated on the northern edge of the so-called “Pacific Ring of Fire,” a 40,000-km-long horseshoe-shaped assemblage of continental landmasses and islands bordering the Pacific Ocean basin that contains many of the world’s active and dormant volcanoes. Schaefer et al. (2009) listed 27 historically active volcanoes in the Aleutian Islands, of which nine have had at least one major eruptive event since 1990. Volcanic eruptions are often significant natural disturbances, and ecosystem responses to volcanic eruptions may vary markedly with eruption style (effusive versus explosive), frequency, and magnitude of the eruption as well as isolation of the disturbed sites from potential colonizing organisms (del Moral and Grishin, 1999). Despite the relatively high frequency of volcanic activity in the Aleutians, the response of island ecosystems to volcanic disturbances is largely unstudied because of the region’s isolation. The only ecological studies in the region that address the effects of volcanic activity were done on Bogoslof Island, a remote, highly active volcanic island in the eastern Aleutians, which grew from a submarine eruption in 1796 (Merriam, 1910; Byrd et al., 1980; Byrd and Williams, 1994). Nevertheless, in the 214 years of Bogoslof’s existence, the island has been visited only intermittently.

Kasatochi Island is a small (2.9 km by 2.6 km, 314 m high) volcano in the central Aleutian Islands of Alaska (52.17°N latitude, 175.51°W longitude; Fig. 1) that erupted violently on 7–8 August 2008 after a brief, but intense period of precursory seismic activity (Scott et al., 2010 [this issue]; Waythomas et al., in review). The island is part of the Aleutian arc volcanic front, and is an isolated singular island. Although the immediate offshore areas are relatively shallow (20–50 m water depth), the island is about 10 km south of the 2000 m isobath, north of which, ocean depths

increase markedly. Kasatochi is located between the deepwater basin of the Bering Sea to the north and shallower areas of intense upwelling in Atka and Fenimore Passes in the North Pacific Ocean to the south. This area apparently produces high marine productivity based on concentrations of feeding marine birds and mammals (see Drew et al., 2010 [this issue]). Kasatochi is about 85 km northeast of Adak, the nearest community and a regional transportation hub, and about 19 km northwest of the western end of Atka Island. The nearest historically active volcanoes are Great Sitkin volcano, about 35 km to the west, and Korovin volcano on Atka Island, about 94 km to the east. Koniuji Island, another small volcanic island, is located about 25 km east of Kasatochi (Fig. 1).

Kasatochi Island is one of nine annual monitoring sites for seabirds in the Alaska Maritime National Wildlife Refuge (Byrd, 2007) and, despite its small size, supported a diverse and remarkably abundant terrestrial and marine flora and fauna (see other papers in this issue). The effects of the 7–8 August 2008 eruption on the island’s ecosystems appeared to have been catastrophic based on a brief field reconnaissance on 22–23 August 2008 by geologists and biologists (Waythomas et al., in review). Deposits of volcanoclastic debris and tephra, some tens of meters thick, covered the island, which formerly had a lush assemblage of low-growing herbaceous and graminoid plants. Pyroclastic flows affected all sides of the island and extended the former coastline about 400 m seaward, increasing the diameter of the island by roughly 30%. The only signs of life following the eruption were a few glaucous-winged gulls (*Larus glaucescens*) seen on the still-warm deposits and some Steller sea lions (*Eumetopias jubatus*) hauled out on a new beach.

The eruption of Kasatochi was unusual in two ways. First, the entire island, including all vegetation and nesting habitats for



**FIGURE 1.** Location of Kasatochi Island in the west-central Aleutian Islands of Alaska. Also shown are nearby islands and extent of ash fall from the 7–8 August 2008 eruption.

birds, and former intertidal and shallow subtidal habitats, were covered by thick volcanic deposits in contrast to larger Aleutian islands where effects of eruptions are more localized and plants and animals in areas little disturbed by eruptive processes are potential sources of immigrants to newly created substrates. The ubiquitous pyroclastic deposits and their mode of emplacement at Kasatochi appeared to have destroyed all organisms and their biophysical habitats. However, the rate of post-eruption erosion and potential for exhumation of viable propagules and organisms (i.e., *in situ* survival) was unknown. Thus the potential role of biological legacies (Franklin, 2005) in the island's recovery compared to the role of colonizers from other islands remains an important question.

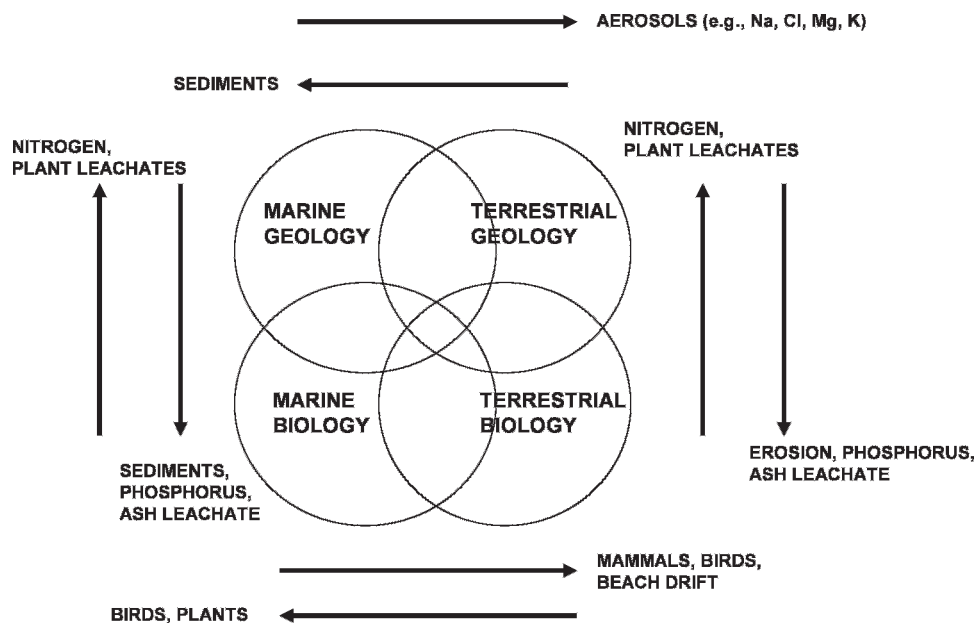
The second unusual circumstance surrounding the Kasatochi eruption is the relative abundance of pre-eruption ecological information obtained over several decades of study (e.g., Drummond, 2006; Bucheit and Ford, 2008). The results of these studies will provide a basis for evaluating the impacts of the eruption on the biota and subsequent ecological succession, similar to studies done elsewhere (e.g., the Krakatau Islands—Whittaker et al., 1989, 1992; Surtsey—Fridriksson and Magnússon, 1992; Jakobsson et al., 2009; and Mount St. Helens—Dale et al., 2005).

Studying the consequences of the Kasatochi eruption will enhance existing knowledge regarding disturbance ecology and primary successional processes following volcanic and other types of disturbance (Walker and del Moral, 2003). These issues include: (1) the role of erosion in determining topographic features (Newhall and Punongbayan, 1997), the types, amounts, and

spatial distribution of residuals (survivors) released from burial (Zobel and Antos, 1992; Antos and Zobel, 2005), site amelioration and creation of safe sites (Walker and del Moral, 2008); (2) the influence of various dispersal modes on early colonization of the new terrestrial and marine habitats (Thornton et al., 2001); (3) the two-way interaction of large bird colonies on newly exposed surfaces and of those surfaces on bird behavior (Magnússon et al., 2009; Petersen, 2009), and (4) the way in which ecosystems reassemble after a major disturbance (Weiher and Keddy, 1999). The Kasatochi eruption provides an excellent opportunity to address these issues and determine the relative roles they have in the structure and functioning of terrestrial and nearshore marine ecosystems in the context of the dynamic volcanism of the Aleutian Islands.

Prior to visiting Kasatochi during summer 2009, we had many questions about the island and its inhabitants. How had the island changed since our brief visit in August 2008? How would the wet, windy Aleutian winter influence erosion and redeposition of sediments? Would nesting birds return and would they find suitable nesting habitat? Did biological legacies in the form of roots, rhizomes, seeds, soil biota, and arthropods survive? What organisms would be among the first to recolonize Kasatochi and from where would they originate? Did nearshore marine waters provide refugia for benthic organisms?

This special issue on the short-term consequences of the 2008 eruption of Kasatochi Island in the Aleutian Islands, Alaska, answers many of these questions and documents the immediate impacts of the eruption on geological, biological, terrestrial, and



**FIGURE 2.** Conceptual model depicting interplay of marine and terrestrial influences that will affect the ecological response and recovery following the Kasatochi eruption.

aquatic features of the island. Three of the papers are primarily geological. Scott et al. (2010) describe the eruption, the geology, and what the pyroclastic materials and rocks on the island tell us about the 2008 eruption. Waythomas et al. (2010) describe how surface and coastal erosion have altered the island's topography and shoreline. Wang et al. (2010) characterize the chemical composition of the pyroclastic deposits both immediately after the eruption and one year later, and describe the conditions that led to exposure of remnant soils. The geological papers set the scene for five papers that describe the biological impacts. Talbot et al. (2010) describe the extensive devastation that occurred to plant communities, and unanticipated plant legacies that survived the eruption. Sikes and Slowik (2010) summarize their pre- and post eruption observations of terrestrial arthropods. They also found survivors and hypothesize a shift in food webs for the diminished arthropod community on the island. Williams et al. (2010) document the effects of the eruption on the avian and mammalian faunas. In the nearshore, Jewett et al. (2010) summarize their observations of a simplified benthic ecosystem that must look remarkably unlike what it did before the eruption. Drew et al. (2010) investigate if signals of the eruption were evident one year later in oceanic nutrients and in the distribution and abundance of marine birds near the island. Lastly, del Moral (2010) provides a synthesis and a broader geographical and theoretical context for our observations and sets the stage for what we intend will be a much longer term study of this disturbance.

### Conceptual Approach and Overall Study Design

To ensure an integrated approach to evaluate the effects of the Kasatochi eruption on island and marine ecosystems, we held a workshop in May 2009 to develop a conceptual model for our study to help define the key study components (Fig. 2), and develop a sampling strategy that integrated marine and terrestrial, as well as physical and biological components.

We view Kasatochi Island as composed of four interconnecting circles representing geological and biological components and processes for both marine and terrestrial ecosystems (Fig. 2). Deposition of hot, pyroclastic material over the entire surface of Kasatochi Island and in the nearshore marine zone out to at least the 20 m isobath was the most significant mechanism of

disturbance of the eruption. The subsequent movement and leaching of these materials will strongly influence responses of Kasatochi Island ecosystems. Erosion of Kasatochi Island sediments into the nearshore marine zone and marine aerosols that deposit small quantities of sodium chloride, iodine, magnesium, potassium, and perhaps other minerals on the island link the post-eruption terrestrial and marine geology components. Erosion, phosphorus, and ash leachates from new geological deposits contribute to both marine and terrestrial ecosystems while recovering biota contributes nitrogen and plant leachates back to the land and the sea floor. Erosion may have either a destabilizing influence on the establishment of flora and nesting birds or a stabilizing influence on the island through exposure of pre-eruption surfaces and biological legacies in the form of viable seeds, roots, and rhizomes. Marine and terrestrial ecosystems are also linked biologically by the seasonal movements of marine birds and mammals and beach drift from the sea to the island. These are important sources of marine-derived nutrients to the island through excreta, and decomposing carcasses and kelps. Ultimately, re-vegetation through growth and spread of surviving plants and colonizers, with nutrient inputs from marine birds and marine mammals, beach drift, atmospheric deposition, and surviving and colonizing terrestrial arthropods will have a stabilizing influence on Kasatochi Island and increase overall ecosystem complexity. The overall ecological response to the eruption will likely be influenced by a complex interplay of marine and terrestrial influences that will both promote and impede recovery. These may have profound effects on the timing of geological and biological responses in both marine and terrestrial ecosystems (Table 1). For example, continued erosion of deposits from Kasatochi and reworking of those sediments in the nearshore zone will strongly influence and may delay recolonization of the intertidal and subtidal zones by benthic organisms, particularly those that require hard substrates for settlement. Onshore, successful breeding by auklets will require exhumation of rock crevices which auklets require for nesting. Recolonization and breeding by songbirds will require extensive revegetation and colonization by insects and other arthropods. These events may take years.

In 2009, geological research included characterizing the stratigraphic units that were emplaced during the eruption, evaluating erosion and geomorphological changes, and character-

TABLE 1

**Predicted biological and geological responses to the 2008 eruption of Kasatochi Volcano in marine and terrestrial ecosystems. Determination of the actual pace of physical and biological responses will require long-term monitoring.**

Ecosystem		Fast response (less than 2 years)	Medium response (several years)	Slow response (many years)
Geological	Marine	Sedimentation; sediment transport	Sediment consolidation	Shore stabilization
	Terrestrial	Erosion of fines; initiation of drainage networks	Continued development of drainage networks	Shore stabilization
Biological	Marine	Re-establishment of plankton food web; initial colonization of sediments	Re-establishment of kelp forest	Re-establishment of pre-eruption benthic community (e.g. coralline algae)
	Terrestrial	Re-occupation by breeding sea lions and non-nesting birds; dispersal of seeds and insects; recovery of plant and arthropod survivors	Primary plant community development; development of arthropod communities	Continued plant community and organic soil development; re-occupation by breeding landbirds and burrow-nesting seabirds

ization of ash-leachates, new substrates, as well as pre-eruption soil surfaces in a few locations. Before-after comparisons for vegetation, arthropods, birds, and marine mammals on land were based on surveys, including in previously established plots for which we had data from before the eruption. A similar approach was used for nutrients, fish, and marine birds in previously surveyed pelagic transects within 20 km of Kasatochi Island. Comparisons of intertidal and nearshore subtidal organisms used data from transects established during the Alaska Monitoring and Assessment Program in the central Aleutians (Jewett et al., 2008) to gain a perspective of what would have been predicted at Kasatochi before the eruption in similar habitats. Because Kasatochi is relatively small, an effort was made to survey as much of the surface of the island as possible to look for “hotspots” of activity by birds and marine mammals and refugia for plants and arthropods.

We adopted common sampling approaches whenever possible as a way to enhance integration across disciplines. A preliminary post-eruption surficial geologic map prepared by the Alaska Volcano Observatory, based on commercially available high resolution satellite imagery, was used as a common base layer for the multi-disciplinary team. Six transects were systematically established to cover the major geologic and topographic features on the island from the rim of the caldera out to the 20 m depth contour offshore of the island. Along some of these transects sampling of pyroclastic deposits, terrestrial and subtidal biota and offshore nutrients were conducted as logistics allowed.

With a longer term study in mind, the research begun in 2009 will be augmented in the future with sampling from a network of permanent plots in order to maximize integration among data sets and disciplines. Long-term monitoring will be required to elucidate patterns and processes of recovery. Biotic recovery (primary succession) and its interplay with geophysical processes are not easily predictable, so monitoring can enhance our ability to better understand ecological and geological interactions. This knowledge is particularly important where anthropogenic disturbances resemble primary succession and tools for accelerating restoration are desired (Walker and del Moral, 2008). Our interdisciplinary approach helps to identify links among processes and organisms across plant, soil, atmosphere, and water interfaces.

### Acknowledgments

Funding for the inaugural year of studies at Kasatochi Island was provided by the North Pacific Research Board (Project #923), Leslie Holland-Bartels of the U.S. Geological Survey (USGS) Office of the Alaska Regional Executive, the Alaska Maritime National Wildlife Refuge, the USGS Alaska Science Center, and the Alaska Volcano Observatory. We are grateful to Captain Billie Pepper and the crew of the M/V *Tiglux* for safely supporting our field work during four expeditions to Kasatochi Island in 2009.

Lisa Scharf Spittler and Jeff Williams, Alaska Maritime National Wildlife Refuge, provided critical logistic support in the Aleutian Islands. We especially thank Charles Crisafulli for providing insights from his work at Mount St. Helens during our May 2009 workshop. The comments of Charles Crisafulli and Virginia Dale on an earlier version of this manuscript are greatly appreciated. This is contribution 251 of the North Pacific Research Board.

### References Cited

- Antos, J. A., and Zobel, D. B., 2005: Plant responses in forests of the tephra-fall zone. In Dale, V. H., Swanson, F. J., and Crisafulli, C. M. (eds.), *Ecological Responses to the 1980 Eruption of Mount St. Helens*. New York: Springer, 47–58.
- Buchteit, R. M., and Ford, J. C., 2008: Biological monitoring in the central Aleutian Islands, Alaska in 2008: summary appendices. Homer, Alaska: U.S. Fish and Wildlife Service Report, AMNWR 08/12, 141 pp.
- Byrd, G. V., 2007: Seabird monitoring on Alaska Maritime National Wildlife Refuge. In Brewer, R. (ed.), *Community-Based Coastal Observing in Alaska: Aleutian Life Forum 2006*. Fairbanks, Alaska: Alaska Sea Grant College Program, University of Alaska, 39–45.
- Byrd, G. V., and Williams, J. C., 1994: Status and trends of seabirds and marine mammals at Bogoslof Island, Alaska, a National Natural Landmark. U.S. Fish and Wildlife Service Report to the National Park Service under Interagency Agreement No. 9700-4-9025. AMNWR 94/10, 9 pp.
- Byrd, G. V., Divoky, G. J., and Bailey, E. P., 1980: Changes in marine bird and mammal populations on an active volcano in Alaska. *Murrelet*, 61: 50–62.
- Dale, V. H., Swanson, F. J., and Crisafulli, C. M. (eds.), 2005: *Ecological Responses to the 1980 Eruption of Mount St. Helens*. New York: Springer, 342 pp.
- del Moral, R., 2010: The importance of long-term studies of ecosystem reassembly after the eruption of the Kasatochi Island volcano. *Arctic, Antarctic, and Alpine Research*, 42: 335–341.
- del Moral, R., and Grishin, S. Y., 1999: Volcanic disturbances and ecosystem recovery. In Walker, L. R. (ed.), *Ecosystems of Disturbed Ground, Ecosystems of the World Vol. 16*. Amsterdam: Elsevier, 137–160.
- Drew, G. S., Dragoo, D. E., Renner, M., and Piatt, J. F., 2010: At-sea observations of marine birds and their habitats before and after the 2008 eruption of Kasatochi Volcano, Alaska. *Arctic, Antarctic, and Alpine Research*, 42: 325–334.
- Drummond, B. A., 2006: Biological monitoring in the central Aleutian Islands, Alaska in 2006: summary appendices. U.S. Fish and Wildlife Service Report, AMNWR 06/06, 125 pp.
- Franklin, J. F., 2005: Reconfiguring disturbance, succession, and forest management: the science of Mount St. Helens. In Dale, V. H., Swanson, F. J., and Crisafulli, C. M. (eds.), *Ecological Responses to the 1980 Eruption of Mount St. Helens*. New York: Springer, v–vii.

- Fridriksson, S., and Magnússon, B., 1992: Development of the ecosystem on Surtsey with reference to Anak Krakatau. *GeoJournal*, 28: 287–291.
- Jakobsson, S. P., Magnússon, B., and Gunnarson, K. (eds.), 2009: *Surtsey Research 12*. Reykjavik, Iceland: Surtsey Research Society, 170 pp.
- Jewett, S. C., Brewer, R., Chenelot, H., Clark, R., Dasher, D., Harper, S., and Hoberg, M., 2008: Scuba techniques for the Alaska Monitoring and Assessment Program (AKMAP) of the Aleutian Islands. In Bruggeman, P., and Pollock, N. W. (eds.), *Diving for Science 2008. Proceedings of the 27th American Academy of Underwater Sciences Symposium*. Dauphin Island, Alabama: American Academy of Underwater Sciences, 71–89.
- Jewett, S. C., Bodkin, J. L., Chenelot, H., Esslinger, G. G., and Hoberg, M. K., 2010: The nearshore benthic community of Kasatochi Island, one year after the 2008 volcanic eruption. *Arctic, Antarctic, and Alpine Research*, 42: 315–324.
- Magnússon, B., Magnússon, S. H., and Fridriksson, S., 2009: Developments in plant colonization and succession on Surtsey during 1999–2008. *Surtsey Research*, 12: 57–76.
- Merriam, C. H., 1910: Bogoslof: our newest volcano. In Dall, W. H., Keeler, C., Ferno, B. E., Gannett, H., Brewer, W. H., Merriam, C. H., Grinnell, G. B., and Washburn, M. L. (eds.), *Harriman Alaska Series, Vol. II History, Geography, Resources*. Washington, D.C.: Smithsonian Institution, Publication 1991, 291–336.
- Newhall, C. G., and Punongbayan, R. S., 1997: *Fire and Mud: Eruptions and Lahars of Mount Pinatubo, Philippines*. Seattle: University of Washington Press.
- Petersen, A., 2009: Formation of a bird community on a new island, Surtsey, Iceland. *Surtsey Research*, 12: 133–148.
- Schaefer, J. R., Cameron, C. E., and Nye, C. J., 2009: *Historically Active Volcanoes of Alaska*. Alaska Department of Natural Resources, Division of Geological & Geophysical Surveys, Miscellaneous Report MP 133, 1 pp.
- Scott, W. E., Nye, C. J., Waythomas, C. F., and Neal, C. A., 2010: August 2008 eruption of Kasatochi Volcano, Aleutian Islands, Alaska—Resetting an island landscape. *Arctic, Antarctic, and Alpine Research*, 42: 250–259.
- Sikes, D. S., and Slowik, J., 2010: Terrestrial arthropods of pre- and post-eruption Kasatochi Island, Alaska, 2008–2009: a shift from a plant-based to a necromass-based food web. *Arctic, Antarctic, and Alpine Research*, 42: 297–305.
- Talbot, S. S., Talbot, S. L., and Walker, L. R., 2010: Post-eruption legacy effects and their implications for long-term recovery of the vegetation on Kasatochi Island, Alaska. *Arctic, Antarctic, and Alpine Research*, 42: 285–296.
- Thornton, I. W. B., Cook, S., Edwards, J. S., Harrison, R. D., Schipper, C., Shanahan, M., Singadan, R., and Yamuna, R., 2001: Colonization of an island volcano, Long Island, Papua New Guinea, and an emergent island, Motmot, in its caldera lake. VII. Overview and discussion. *Journal of Biogeography*, 28: 1389–1408.
- Walker, L. R., and del Moral, R., 2003: *Primary Succession and Ecosystem Rehabilitation*. Cambridge: Cambridge University Press, 442 pp.
- Walker, L. R., and del Moral, R., 2008: Lessons from primary succession for restoration of severely damaged habitats. *Applied Vegetation Science*, 12: 55–67.
- Wang, B., Michaelson, G., Ping, C.-L., Plumlee, G., and Hageman, P., 2010: Characterization of pyroclastic deposits and pre-eruptive soils following the 2008 eruption of Kasatochi Island volcano, Alaska. *Arctic, Antarctic, and Alpine Research*, 42: 276–284.
- Waythomas, C. F., Scott, W. E., and Nye, C. J., 2010: The geomorphology of an Aleutian volcano following a major eruption: the 7–8 August 2008 eruption of Kasatochi Volcano, Alaska, and its aftermath. *Arctic, Antarctic, and Alpine Research*, 42: 260–275.
- Waythomas, C. F., Scott, W. E., Nye, C. J., Prejean, S. G., Izbekov, P., and Schneider, D. J., In review: The August 7–8, 2008 eruption of Kasatochi volcano, central Aleutian Islands, Alaska. *Journal of Geophysical Research*.
- Weihner, E., and Keddy, P. (eds.), 1999: *Ecological Assembly Rules: Perspectives, Advances and Retreats*. Cambridge: Cambridge University Press, 418 pp.
- Whittaker, R. J., Bush, M. B., and Richards, K., 1989: Plant recolonization and vegetation succession on the Krakatau Islands, Indonesia. *Ecological Monographs*, 59: 59–123.
- Whittaker, R. J., Bush, M. B., Asquith, N. M., and Richards, K., 1992: Ecological aspects of plant colonization of the Krakatau Islands. *GeoJournal*, 28: 201–211.
- Williams, J. C., Drummond, B. A., and Buxton, R. T., 2010: Initial effects of the August 2008 volcanic eruption on breeding birds and marine mammals at Kasatochi Island, Alaska. *Arctic, Antarctic, and Alpine Research*, 42: 306–314.
- Zobel, D. B., and Antos, J. A., 1992: Survival of plants buried for eight growing seasons by volcanic tephra. *Ecology*, 73: 698–701.

MS accepted May 2010