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RESEARCH ARTICLE

Biological responses of Crested and Least auklets to volcanic destruction of nesting habitat in the Aleutian Islands, Alaska

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ABSTRACT

Crested Auklets (*Aethia cristatella*) and Least Auklets (*A. pusilla*) are crevice-nesting birds that breed in large mixed colonies at relatively few sites in the Aleutian Island archipelago, Bering Sea, Gulf of Alaska, and Sea of Okhotsk. Many of these colonies are located on active volcanic islands. The eruption of Kasatochi volcano, in the central Aleutians, on August 7, 2008, completely buried all crevice-nesting seabird habitat on the island. This provided an opportunity to examine the response of a large, mixed auklet colony to a major geological disturbance. Time-lapse imagery of nesting habitat indicated that both species returned to the largest pre-eruption colony site for several years, but subsequently abandoned it within 5 yr after the eruption. In 2010, a rockfall site in a cove north of the old colony site began to accumulate talus, and groups of auklets were observed using the site in 2011. Use of the new colony appeared to coincide with the abandonment of the old colony site by both species, though surface counts suggested that Least Auklets shifted to the new colony sooner than Crested Auklets. At-sea surveys of seabirds before and after the eruption indicated that both Crested and Least auklets shifted their at-sea distributions from the waters around Kasatochi Island to nearby Koniuji Island. In combination, at-sea counts and colony time-lapse imagery indicated that Crested and Least auklets using Kasatochi responded to the volcanic disturbance and complete loss of nesting habitat at the main colony on Kasatochi with dispersal either to newly created habitat on Kasatochi or to an alternate colony on a nearby island.

Keywords: *Aethia cristatella*, *A. pusilla*, Crested Auklet, dispersal, eruption, Least Auklet, nesting, talus

Réponses biologiques d'*Aethia cristatella* et *Aethia pusilla* à la destruction volcanique de l'habitat de nidification dans les Aléoutiennes, en Alaska

RÉSUMÉ

Aethia cristatella et *Aethia pusilla* sont des oiseaux nichant en grandes colonies mixtes dans des crevasses, à relativement peu de sites dans la chaîne aléoutienne, la mer de Béring, le golfe d'Alaska et la mer d'Okhotsk. Plusieurs de ces colonies se trouvent sur des îles volcaniques actives. Le 7 août 2008, l'éruption du volcan Kasatochi dans le centre des Aléoutiennes a complètement enseveli l'habitat des oiseaux marins nichant dans des crevasses sur l'île, fournissant une occasion d'examiner la réponse d'une grande colonie mixte d'*Aethia* sp. face à une perturbation géologique majeure. L'imagerie en accéléré de l'habitat de nidification indique que les deux espèces sont retournées au plus grand site pré-éruption de la colonie pendant quelques années, puis ont complètement abandonné le site moins de 5 ans après l'éruption. En 2010, un site d'éboulement rocheux situé dans une anse au nord de l'ancien site de la colonie a commencé à accumuler un talus d'éboulis. Des groupes d'*Aethia* sp. ont été observés utilisant le site en 2011. L'utilisation de la nouvelle colonie semblait coïncider avec l'abandon de l'ancien site de la colonie par les deux espèces, bien que les dénombrements en surface suggèrent qu'*A. pusilla* ait changé pour la nouvelle colonie plus tôt qu'*A. cristatella*. Les dénombrements en mer d'oiseaux marins avant et après l'éruption ont indiqué que les deux espèces ont changé leur distribution en mer, passant des eaux entourant Kasatochi aux environs de l'île Koniuji. La combinaison des dénombrements en mer et de l'imagerie en accéléré de la colonie a indiqué que les individus des deux espèces utilisant Kasatochi répondaient à la perturbation volcanique et à la perte complète de l'habitat de nidification de la principale colonie sur Kasatochi par la dispersion vers un habitat nouvellement créé sur Kasatochi ou vers une colonie alternative sur une île voisine.

Mots-clés : *Aethia cristatella*, *Aethia pusilla*, dispersion, éruption, nidification, talus d'éboulis

INTRODUCTION

Crested Auklets (*Aethia cristatella*) and Least Auklets (*A. pusilla*), hereafter collectively referred to as “auklets,” nest together primarily in large colonies on a small number of remote islands in the Aleutian island archipelago, Bering and Chukchi Seas, Gulf of Alaska, and Sea of Okhotsk. These islands provide crevice-nesting habitat (i.e. vegetation-free rubble and talus slopes formed by rockfalls) (Bédard 1969, Knudtson and Byrd 1982, Piatt et al. 1990) and lava flows (Day et al. 1979, Major et al. 2006), which are commonly found on active volcanic islands. In addition to providing nesting habitat, auklet colony islands are—by necessity—located in proximity to foraging areas with persistent and abundant zooplankton prey resources (Hunt et al. 1993, 1998, Piatt and Springer 2003). The limited availability of nesting areas with sufficient crevice-nesting habitat and persistent local prey resources likely accounts for the relative scarcity of auklet colonies, despite being the most abundant breeding seabirds in the region (Jones and Montgomerie 1991). The 8.6 million Least Auklets and 6.4 million Crested Auklets in the combined Alaska–Russia region use only 52 known colonies (Renner et al. 2017).

For auklets, suitable nesting habitat is a continually changing resource that does not persist; the deposition of biological debris, creation of soil, and encroachment of vegetation eventually fill the crevices, making the habitat unsuitable for nesting (Bédard 1969, Roby and Brink 1986, Jones and Hart 2006, Renner et al. 2017). Therefore, the renewal of nesting habitat depends on periodic physical disturbance. Volcanically active areas in the Aleutian Islands are intermittently affected by eruptions occurring at the temporal scale of tens to hundreds of years (Waythomas 2015). There is a lack of knowledge regarding the dispersal of species, such as auklets, that require disturbances to maintain or create nesting habitat. With so few colonies, understanding the resiliency of these populations to rapid habitat change is vital to sound management in a future increasingly shaped by natural and anthropogenic perturbations. The eruption of a volcanic island within the Alaska Maritime National Wildlife Refuge, with large nesting populations of auklets, presented an opportunity to follow the response of auklets to such a disturbance.

Kasatochi volcano in the central Aleutian Islands erupted on August 7, 2008. The resulting ash and pyroclastic flows blanketed the island, covering terrestrial habitats to a depth of 15–20 m but did not produce any lava flows (Waythomas et al. 2010). Thus, Kasatochi Island provided a natural laboratory to follow the aftereffects of a large-scale disturbance to nesting habitats. The terrestrial changes resulting from the eruption included the removal or burial of any suitable nesting habitat for an estimated

100,000 Crested Auklets and 150,000 Least Auklets nesting on the island (Williams et al. 2010). The eruption occurred after the majority of auklet chicks should have fledged and moved off shore (Drummond and Larned 2007). Hence, most adults and some juveniles may have escaped catastrophic mortality. This conclusion was supported by observations of large flocks of auklets returning to the slopes of the main colony in 2009, as well as at-sea auklet density data collected around Kasatochi before and after the eruption (Drew et al. 2010). Because both species exhibit high levels of nest-site fidelity (Jones and Montgomerie 1991, Gaston and Jones 1998), the return of auklets to the main colony site in 2009 was not, in itself, an indication that successful breeding would occur. Indeed, despite their return, the complete loss of nesting habitat left the continued use of Kasatochi by auklets in doubt for the future.

While nest-site fidelity is a viable life-history strategy for seabirds nesting in relatively stable environments, auklets also rely on disturbance over moderate to long periods to replenish nesting habitat (Renner et al. 2017). This paradox appears to present a dilemma for the generation of birds that bridge the disturbance. While auklets have shown the ability to disperse to new colonies on the same island, there has been no evidence indicating their ability to move to new islands (Renner et al. 2017). Following the eruption on Kasatochi, we hypothesized that auklets from the Kasatochi colony had 3 options: (1) They could maintain their fidelity to traditional colony site(s) on Kasatochi, as indicated by continued attendance at the primary colony site and slowly decreasing at-sea densities around Kasatochi. (2) They could disperse (emigrate) from Kasatochi, as indicated by rapid declines in attendance at the old colony site and shifts in at-sea density from Kasatochi toward nearby Koniuiji. Or (3) they could disperse within the same island, relocating on Kasatochi to newly developed talus piles or beach boulders, as indicated by rapid declines in attendance at the old colony site, use of new alternative on-island sites, and a stabilization of at-sea densities. These hypotheses were not mutually exclusive. In combination, changes in at-sea data, Kasatochi attendance data, and ground observations allowed us to assess our conceptual framework (Table 1).

METHODS

Study Area

Kasatochi Island (52.1693N, –175.1131W) is a roughly circular island volcano located in the central Aleutian archipelago, 80 km northeast of Adak Island. As a result of the eruption on August 7, 2008, the island grew in land area from 5.0 to 6.9 km². Nearby Koniuiji Island (52.2204N, –175.1321W; 0.8 km²) is a nascent stratovolcano 25 km east of Kasatochi (Figure 1). Atka and Fenimore passes,

TABLE 1. Conceptual model of Crested and Least auklet responses following the 2008 eruption, indicating the expected results for each hypothesis if true.

Hypothesis	Kasatochi		Koniuji
	At-sea density	Colony attendance	At-sea density
1: Colony fidelity	Decrease	Slow decline	No change
2: Emigration	Decrease	Rapid decline	Increase
3: Relocation	No change	Rapid decline	No change

20–30 km south of the islands, provide persistent tidally driven upwellings that support high primary production (Ladd et al. 2005a, Mordy et al. 2005) and large numbers of marine birds (Ladd et al. 2005b). The primary pre-eruption colony site was in Tundering Cove on the northwest side of the island (Figure 2).

Coastal Reconnaissance

Each year that we visited Kasatochi, we conducted a shoreline circumnavigation to visually assess changes to the island. Where it was possible to land, we investigated sites where auklets were observed socializing or where there were signs of recent auklet use (i.e. guano on rocks). We searched these areas for signs of auklet nesting in and below surface crevices. Although these efforts were opportunistic, we were able to determine, where access to sites was available, whether auklets were attempting to nest.

Colony Attendance

We installed a time-lapse camera (Canon 40D with a 100 mm focal length) in June 2010 to photograph the “Tundering Talus” colony in Tundering Cove, the largest auklet colony site on the island prior to the eruption (Figure 1). The camera was set up 200 m across from the

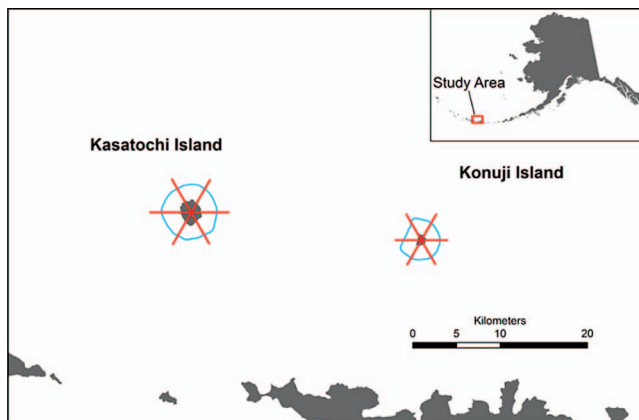


FIGURE 1. Location of the study area in the central Aleutian Islands. Blue circles represent circumnavigation survey tracks. Red spokes show our splitting of annual circumnavigations into transect segments.

original colony site. The field of view included areas used for plot counts prior to the eruption (Williams et al. 2010). A series of deep-cycle batteries and a solar charging panel provided power to the camera. During the summers of 2010, 2012, and 2013, the camera collected images of the Tundering Cove colony. We were not able to collect imagery in 2011 because of equipment failure. The camera collected images from a section of the slope $\sim 60 \times 90$ m in 15 min intervals. Given the distance, weather, and typical lighting conditions, accurate identification of auklets to species was limited to a small subset of images. This species-specific subset was used to identify the proportionate representation of Crested and Least auklets. Surface counts of auklets tend to be difficult to compare because observers record only birds that are above ground (Renner et al. 2006). To quantify auklets on images, hereafter referred to as “attendance,” we overlaid a 4×6 cell grid over each image and counted presence–absence of auklets for each cell. We converted the total number of cells with auklets of either species to a percentage for our “attendance” metric. We excluded images where all cells ($n = 24$) could not be assessed because of lighting conditions, fog, or rain. We assessed all images between June 19 and July 15 for 2010, 2012, and 2013. Given natural mortality and a lack of reproduction, we expected attendance at the old colony site to drop over time. To model auklet populations through time, we used a combined survival

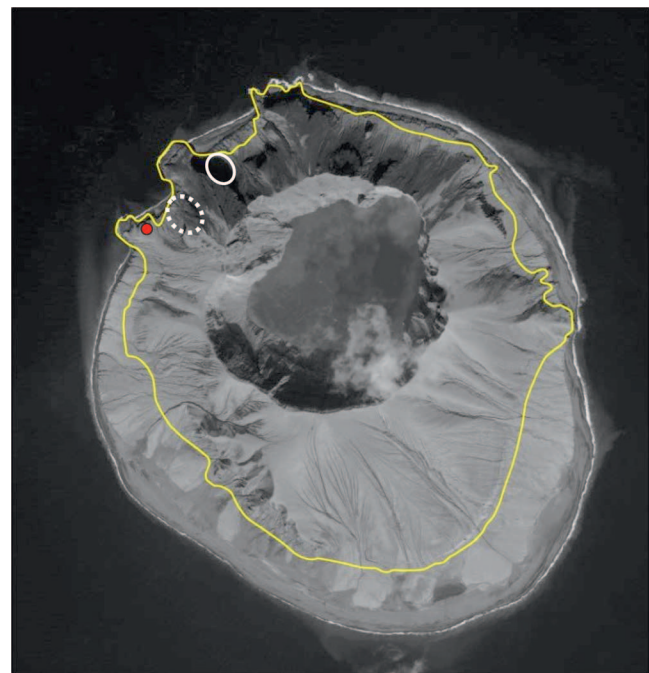


FIGURE 2. Location of Tundering Cove colony (dashed white circle), the time-lapse camera (red dot), and Whiskey Cove colony (solid white circle) on Kasatochi Island. The yellow line represents the pre-eruption coastline.

rate of 0.84 for both auklet species, based on previously calculated estimates (made using Program MARK) of 0.844 for Crested Auklets and 0.848 for Least Auklets on Kasatochi during 1996–2007 (Drummond and Larned 2007). Pooled 95% confidence intervals were constructed using previously calculated standard errors (Drummond and Larned 2007).

In 2012 we placed a small commercial time-lapse camera (Reconyx UltraFire) at the new colony site in Whiskey Cove as a pilot project to test the capabilities of the hardware for assessing auklet activity. We used this camera to assess the comparative proportions of Crested and Least auklets at the new colony site. We made surface counts of auklets in an area about 5×3 m directly in front of the camera. Images were collected every minute, but we looked only at images separated by ≥ 5 min and ignored images where identification to species was not possible. No data were collected in 2013 because we could not get access to the site, as a result of erosion below the new colony.

At-sea Seabird Surveys

Prior to the eruption (1996 and 2005), we conducted circumnavigations of Kasatochi and Koniuji islands at a distance of 1.8 km from shore as part of a broader survey of bird distribution in the area. Circumnavigations around each island were split into 6 sections that were sampled annually (Figure 1). Following the Kasatochi eruption, we conducted surveys, with identical tracks, around Kasatochi and Koniuji in 2009, 2014, and 2016. In 2012, only Kasatochi was surveyed because of time limitations. We conducted all surveys from the *R/V Tiglax* using standard protocols (Gould and Forsell 1989), though the post-eruption surveys used a modified method for counting flying birds. Vessel speeds varied slightly, from 9 knots in 1996 and 2005 to 7 knots in 2009, 2014, and 2016. Two observers, stationed on the flying bridge (one on each side of the ship), continuously recorded all birds observed on the water within 150 m on both sides and 300 m in front of the vessel. We counted flying birds using instantaneous scans (Gould and Forsell 1989). Pre-eruption surveys (1996 and 2005) used a window 300 m forward and 150 m to each side for birds on the water and 3 min interval between snapshot counts, while for the post-eruption surveys the window for snapshot counts was reduced to 150 m forward and 150 m to each side (combined 150×300). This change followed the revised U.S. Fish and Wildlife Service survey protocols (K. Kultz personal communication). The new protocol compensated for the shortened observation window by shortening the time interval between snapshots (~ 1 min, depending on speed). These changes minimize unseen flying birds and maximize identification of flying birds. Although the area surveyed in the pre- and post-surveys of flying birds was equivalent,

the better identification allowed by the shorter window may have had a minimal positive effect on densities. Even if there was a slight positive effect, it would have had no effect on comparisons between islands. Sightings were recorded using a computer-based system (dLOG; R.G. Ford Consulting, Portland, Oregon, USA), which assigned GPS positions to observations in real time and recorded track line positions at 30 s intervals.

Data Analysis

We used attendance of Crested and Least auklets from time-lapse images to test for changes in annual colony occupancy at the “Tundering Talus” site between 2010 and 2013. These data had skewed distributions due to the extremely high number of zero values (where no birds were present), so we used a Kruskal-Wallis rank-sum test followed by a post hoc Dunn test to identify which years were different. We calculated the coefficient of variation (CV) within each year’s attendance counts from images, further clarifying attendance patterns among years. Higher CVs would indicate increasingly erratic use within a particular breeding season, whereas lower CVs would indicate more consistent use (Hatch and Hatch 1989). Given sample sizes, expected and observed attendance were not tested statistically, but a qualitative assessment was possible.

We tested for changes in at-sea densities for each auklet species following the eruption by using ANOVA (analysis of variance) models. Our models included “eruption” (pre- or post-eruption), “island,” and “transect segment” and their interactions as explanatory variables. Crested and Least auklet densities were \log_{10} transformed to normalize the data.

RESULTS

Island Reconnaissance

In 2009 we visited Kasatochi in July, 11 mo after the eruption. At that time no suitable nesting habitat was visible, but many birds were sitting on the thick layer of ash covering the rocky talus of the Tundering Talus colony site, and we observed large numbers of eggs sitting on the slope unattended. In the following years, no eggs were observed at the old colony site. In 2010 we walked $\sim 80\%$ of the coastline. We located multiple occurrences of auklets on beach boulder fields on the northeast, west, and northwest sides of Kasatochi. We found 3 eggs among beach boulders, but none appeared to be attended. There was no reconnaissance conducted in 2011. In 2012 we investigated a large talus pile in Whiskey Cove, 0.35 km north of the Tundering Cove site of the original colony. From the water, many auklets were visible on the talus. Once ashore, we found large numbers of both Crested and Least auklets nesting in a new (post-eruption) talus pile

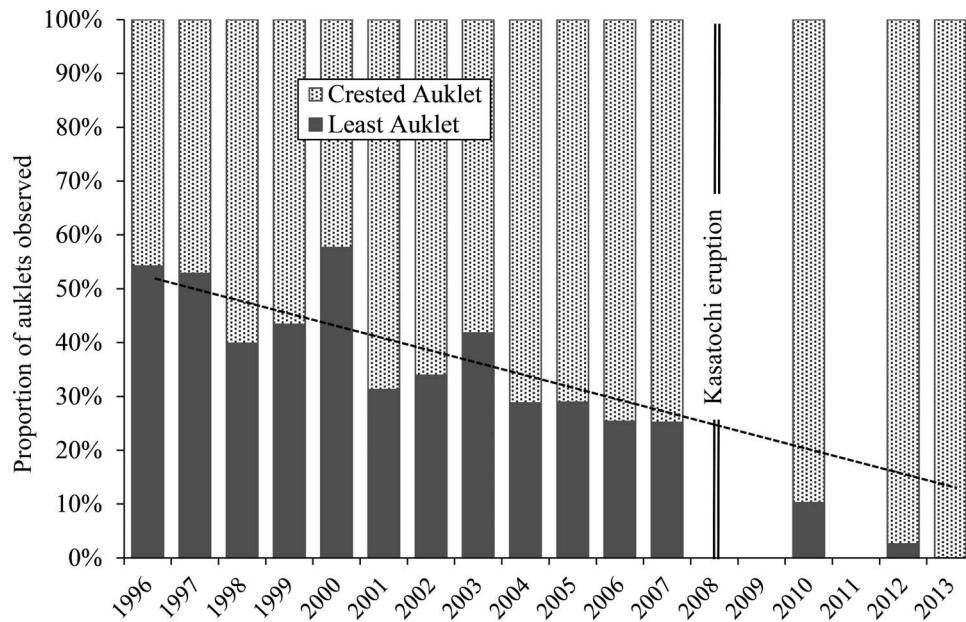


FIGURE 3. Proportion of Crested and Least auklets observed at the old colony site in Tundering Cove, Kasatochi Island, 1996–2013. Pre-eruption counts were made on designated population plots (Drummond and Larned 2007). Post-eruption counts were made from cells of the best available time-lapse camera images. Dashed line represents the trend in the Crested:Least auklet ratio based on the pre-eruption trend.

that had fallen on top of the ash. We were able to revisit the new Whiskey Cove colony site in 2013 and measured its spatial extent at 0.84 ha. Since then, erosion of the coastal bluff has cut off access, preventing additional surveillance from land. We have continued to monitor the Whiskey Cove colony from the water, using repeated photography (2014–2016). From these images, we have determined that this new colony remains highly active and represents the only large nesting area of auklets on the island.

Colony Attendance

A total of 7,418 images of the colony slope were collected between June 19 and July 15 in 2010, 2012, and 2013. No images were collected during 2011 because of an equipment failure. Images collected at night and in poor weather conditions were eliminated, leaving 3,803 images for assessment. Species discrimination was impossible on the majority of images; hence, we used occupied cells from the best images ($n = 72$) to compare proportions of Least to Crested auklets (2010–2013). Pre-eruption plot counts indicated a gradual increase in the proportion of Crested to Least auklets between 1996 and 2007 (Drummond and Larned 2007). Our counts based on imagery indicated an acceleration of this trend for both species, with Least Auklets disappearing completely from the old colony site by 2013 (Figure 3). The post-eruption combined attendance (both species) differed significantly among years (Kruskal-Wallis rank-sum test, $U = 111.04$, $df = 2$, $P < 0.001$). Average auklet attendance decreased

annually, from a high of 6.7% of occupied cells in 2010 to a low of 0.17% in 2013. Attendance declined significantly each year at the old colony from 2010 to 2013 (Dunn's test $P < 0.05$) while within-year CV increased markedly (Table 2). Given the lack of reproductive habitat at the former colony site, we expected no recruitment, but the declines in attendance could have been due to dispersal or mortality. We modeled expected declines due to mortality by using pre-eruption adult survivorship studies at Kasatochi during 1996–2007 (Drummond and Larned 2007). Using 2009 as a baseline, and a mean combined annual survival rate of 84% for Crested and Least auklets, we estimated that by 2013, attendance should decline to ~59% of that observed in 2009. Instead, we saw an ever decreasing level of attendance on the colony slope, with the final year 2012–2013 down to 2.5% of the 2009 baseline (Figure 4).

In 2013 a total of 180 images with birds were collected by time-lapse camera over 5 days at the Whiskey Cove colony and were assessed for surface counts of Crested and

TABLE 2. Average annual occupancy of the old Tundering Talus colony site. All years were significantly different (Dunn's test, $P < 0.05$). Within-year coefficient of variation (CV) indicated more erratic use of the old colony over time.

Year	n	Mean	SD	CV
2010	1,357	1.62	5.34	3.30
2012	1,350	0.64	3.17	4.95
2013	1,096	0.04	0.46	11.14

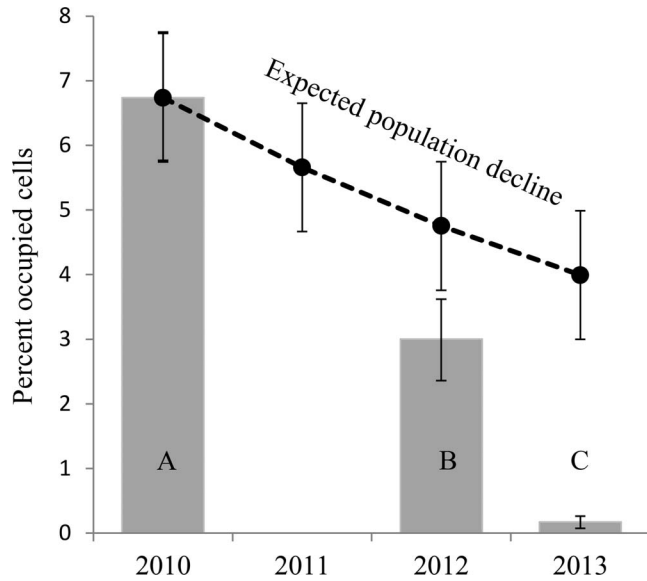


FIGURE 4. Mean and 95% confidence interval (CI) for percentage of photographic grid cells ($n = 24$) with auklets present, June 19–July 15, 2010–2013. Letters indicate significantly different years. Dashed line represents the predicted decline (with 95% CI), assuming pre-eruption survivorship with no recruitment.

Least auklets. In contrast to our results from the old colony site, Least Auklets accounted for 71% of the birds counted, compared to Crested Auklets at 29%.

At-sea Seabird Surveys

At-sea densities of auklets around Koniuji and Kasatochi were sampled twice before the eruption and 3 (Koniuji) or 4 (Kasatochi) times after the eruption. Weather precluded data collection around Koniuji in 2012. At-sea densities of Crested Auklets did not differ between islands, among transect segments, or pre- vs. post-eruption; however, the interaction between island and eruption was significant (Table 3). Following the eruption, densities of Crested Auklets around the Kasatochi colony decreased while densities around the control colony at Koniuji increased (Figure 5).

TABLE 3. Effects of the 2008 eruption on Crested Auklet at-sea densities by island and transect segment, based on analysis of variance. Asterisks indicate significant explanatory variables (* $P < 0.05$).

Source	df	F	P
Eruption	1	0.001	0.99
Segment	5	1.65	0.17
Island	1	0.15	0.70
Eruption × segment	5	0.99	0.43
Eruption × island	1	5.83	0.02*
Segment × island	5	1.23	0.31
Eruption × segment × island	5	0.24	0.94

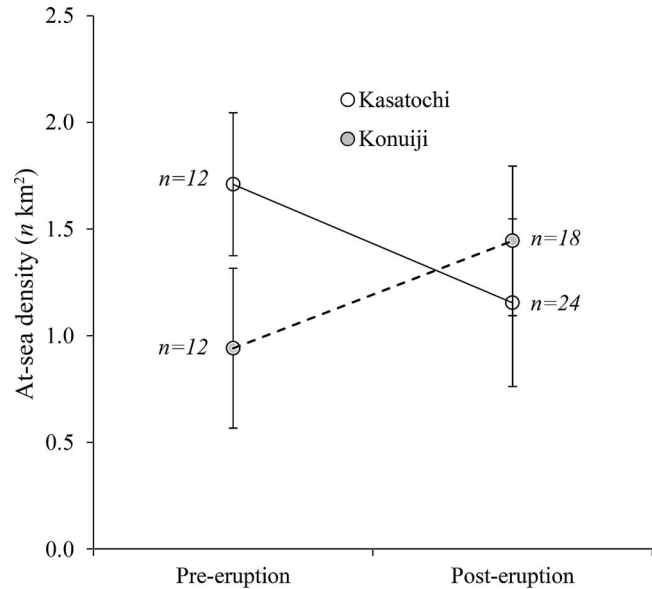


FIGURE 5. Average (\pm SE) at-sea density of Crested Auklets pre-eruption (1996, 2005) and post-eruption (2009–2016). Trend lines connect values from Kasatochi (solid) and Koniuji (dashed) islands. All data were collected in June and July.

For Least Auklets, both eruption and the island × eruption interaction were significant predictive variables for at-sea densities of Least Auklets (Table 4). The interaction term indicates that auklet populations changed differently at each island after the eruption. Neither island nor transect segment were a significant explanatory factor for this species (Table 4). At-sea density of Least Auklets increased following the eruption, particularly around Koniuji. Densities shifted from being higher at Kasatochi before the eruption to being higher at Koniuji after the eruption (Figure 6).

DISCUSSION

On August 7, 2008, the eruption of Kasatochi volcano physically transformed the island, making it a test case for examining the results of large-scale disturbances on Crested and Least auklets, 2 crevice-nesting seabirds that

TABLE 4. Effects of the 2008 eruption on Least Auklet at-sea densities by island and transect segment, based on analysis of variance. Asterisks indicate significant explanatory variables (** $P < 0.01$, *** $P < 0.001$).

Source	df	F	P
Eruption	1	18.20	<0.001***
Segment	5	1.47	0.22
Island	1	0.23	0.63
Eruption × segment	5	1.67	0.16
Eruption × island	1	11.28	0.002**
Segment × island	5	0.56	0.73
Eruption × segment × island	5	0.53	0.75

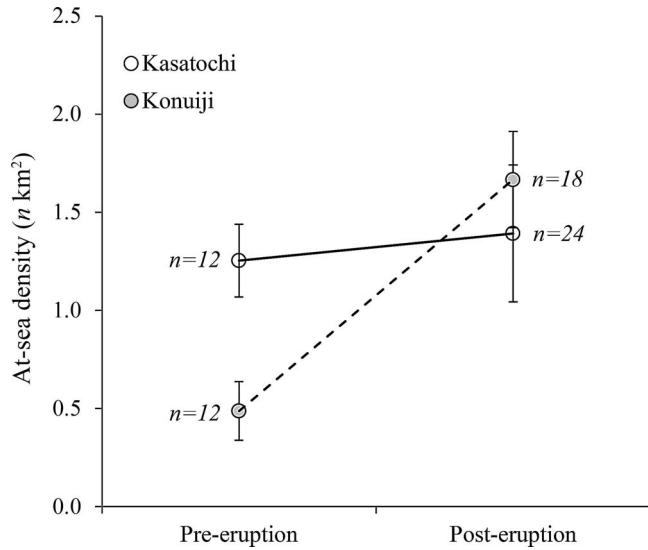


FIGURE 6. Average (\pm SE) at-sea density of Least Auklets pre-eruption (1996, 2005) and post-eruption (2009–2016). Trend lines connect values from Kasatochi (solid) and Koniuji (dashed) islands. All data were collected in June and July.

previously dominated the fauna on Kasatochi Island (Williams et al. 2010). Due to the timing of the eruption, which occurred after most nestlings had fledged ($\sim 85\%$ of Least Auklets and $\sim 60\%$ of Crested Auklets), direct mortality from the disturbance was limited to a minority of that year's chicks (Williams et al. 2010). The eruption provided the setting for a natural experiment to determine how large intact populations of Crested and Least auklets would respond to a sudden and complete loss of local nesting habitat. For a relatively long-lived seabird, the loss of 2–3 yr of reproduction should not be critical to a population, but there should be some threshold for how many years of failed reproduction a population can tolerate. Thus, the long-term viability of auklet populations at Kasatochi after the eruption depended on either their surviving until previous nesting crevices were exposed and made available again or their ability to disperse to alternative sites. We had considered erosion as a potential process to excavate pre-eruption nest sites; however, to date, no pre-eruption nesting habitat has been exposed at the original colony site. Because the eruption was unconsolidated pyroclastic debris, there was no lava—which is also used by auklets in the Aleutian Islands for nesting habitat (Jones 1993)—but the eruption and accompanying earthquakes may have accelerated the process of talus formation.

Despite the return of large numbers of auklets to the Tundering Talus colony site in 2009, which was the first nesting season following the eruption, the lack of nesting habitat and large number of eggs on the surface indicated that there was no successful reproductive effort that

summer. Given that the returning auklets represented a group with strong nesting-site fidelity and no potential for reproductive success at their old colony, we expected population declines in the short term. A lack of nesting sites suggested that immigration would not be a factor. The additional exposure of auklets on the old colony site, devoid of crevices, may have increased predation to some extent. However, in 2009, the auklet predators on the island were either below pre-eruption populations, in the case of Glaucous-winged Gulls (*Larus glaucescens*) and Peregrine Falcons (*Falco peregrinus*), or were unchanged, in the case of Bald Eagles (*Haliaeetus leucocephalus*; Williams et al. 2010). In the subsequent years, we didn't observe a substantial increase in the populations of these predators. This suggests that predation on auklets had not increased; however, we cannot discount the possibility that the lack of crevice habitat led to raised levels of stress on auklets, due to perceived risk or actual increases in harrying by avian predators. We concluded that the abandonment of the colony was due to dispersal, not increased predatory mortality, though the rapid decline in attendance of the old colony site may have been affected by auklets' perceived risk. Although both species left the old colony site, Least Auklets abandoned it more quickly and completely than Crested Auklets. Some nesting attempts by Least Auklets were recorded along the coast of Kasatochi among beach boulders, but no large-scale post-eruption auklet nesting was observed until 2012, when we investigated the results of a post-eruption rockfall in Whiskey Cove sighted in 2011. Field reconnaissance confirmed that thousands of birds were nesting and had established a new colony. The time-lapse data from Whiskey Cove indicated that in 2012, Least Auklets numerically dominated this new colony site at the same time that they had nearly disappeared from the old colony. Our finding that Least Auklets may be more inclined to pioneer new sites than Crested Auklets corroborates anecdotal observations on Gareloi Island, where Least Auklets were noted as having an increased presence on newly revegetated sample plots (Major et al. 2017). Although it was not possible to determine whether recruitment for Crested or Least auklets has recovered to pre-eruption levels, the new colony site demonstrated that auklets' new nesting habitat could be exploited within 2–3 yr.

At-sea densities indicated that both Crested and Least auklets were affected by the 2008 eruption (Figures 5 and 6). Prior to the eruption, at-sea densities of both species were higher around Kasatochi than Koniuji. These densities were likely due to Kasatochi being a larger island (4–5 \times the size of Koniuji) with greater terrestrial habitat available for nesting. Following the 2008 eruption, the relative at-sea densities of Crested Auklets around the 2 islands flipped, such that post-eruption densities were higher on Koniuji than on Kasatochi. At-sea densities of

Least Auklets showed a similar change. Interpretation is slightly complicated by the fact that at-sea densities of Least Auklets around Kasatochi did not change significantly, but the dramatic increase (>300%) in their densities around Koniuji suggested immigration. The early use of the new colony site in Whiskey Cove by Least Auklets may also have affected the at-sea densities, because recruitment may have increased. We didn't have marked birds, so there's no way to definitively determine whether the differences in Crested and Least auklet densities were due to emigration from Kasatochi to Koniuji, though the significant eruption \times island interaction suggests that this was a plausible explanation. Dispersal from Kasatochi would explain the shifted at-sea densities toward the nearby colony at Koniuji; however, the limited nesting habitat at Koniuji suggests that this will not lead to long-term auklet population increases. Suboptimal habitat on Kasatochi following the eruption consisted of a narrow band of beach boulders at several locations along the coast that supported little nesting, often ending in abandoned eggs. Conversely, the new talus pile in Whiskey Cove created \sim 1 ha of new high-quality nesting habitat only 0.3 km from the old colony site. We first noted groups of auklets attending the new site in 2011, coinciding with a rapid abandonment of the old colony site by 2013. This shift to the new Whiskey Cove colony appeared to be more pronounced in Least Auklets, though we don't know whether this greater "first use" by Least Auklets will translate into a different balance in populations of the 2 species over time.

Availability of nesting habitat can be a limiting factor for auklets. Once created, crevice habitats tend to undergo a slow degradation in quality as they fill in with soil, vegetation, and detritus (Major et al. 2017, Renner et al. 2017). The eruption of Kasatochi provided an example of how Crested and Least auklets, and potentially any crevice-nesting seabirds, respond to intense disturbances, highlighting the potential importance of dispersal. This eruption also provided an example of how crevice-nesting habitat may be renewed. Further research on seabirds nesting on disturbed sites should focus on understanding the decisions affecting dispersal and the balance between species sharing limited nesting habitat.

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