VARIATION IN MARINE DISTRIBUTIONS OF CASSIN'S AUKLETS (*PTYCHORAMPHUS ALEUTICUS*) BREEDING AT TRIANGLE ISLAND, BRITISH COLUMBIA

W. Sean Boyd,[1,3] Laura McFarlane Tranquilla,[2,4] John L. Ryder,[2,5] Steven G. Shisko,[1] and Douglas F. Bertram[1,2,6]

[1]*Pacific Wildlife Research Centre, Canadian Wildlife Service, Environment Canada, RR#1, 5421 Robertson Road, Delta, British Columbia V4 K 3N2, Canada; and* [2]*Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia V5A 1S6, Canada*

Abstract.—Approximately 55% of the world's population of Cassin's Auklets (*Ptychoramphus aleuticus*) nests at Triangle Island, British Columbia. To improve our understanding of the biology of these birds during the breeding season, we tracked 112 radiomarked individuals over three years, 1999–2001. We flew high-altitude surveys to describe the at-sea distributions of the marked birds during the chick-rearing period. Using radiotelemetry point locations, we determined that the location of marine use areas, distance from colony, and water depth varied significantly across years. In 1999 and 2000, radiomarked birds were, on average, ~50 km southwest of Triangle Island in waters approximately 1400–1800 m deep. However, in 2001, radiomarked birds were, on average, ~80 km northwest of Triangle Island in waters ~725 m deep. Intra-annually (i.e., between surveys spanning days or weeks), there were no such large-scale directional shifts in marine use area. The size of marine use areas (quantified using kernel home range [KHR] analyses) varied across the three years, from approximately 650 to 1,400 km^2 (50% KHR) and from approximately 3,200 to 8,200 km^2 (95% KHR). *Received 16 August 2006, accepted 3 April 2007.*

Key words: Cassin's Auklet, marine distribution, marine use area, *Ptychoramphus aleuticus*, radiotelemetry, Triangle Island.

Variation des distributions en mer de *Ptychoramphus aleuticus* se reproduisant sur l'île Triangle, en Colombie-Britannique

Résumé.—Approximativement 55% de la population mondiale de *Ptychoramphus aleuticus* niche sur l'île Triangle, en Colombie-Britannique. Afin d'améliorer notre compréhension de la biologie de ces oiseaux durant la saison de reproduction, nous avons suivi 112 oiseaux équipés d'émetteurs pendant trois ans, soit de 1999 à 2001. Nous avons réalisé des inventaires par survol à haute altitude afin de décrire les distributions en mer des oiseaux marqués au cours de la saison d'élevage des poussins. À l'aide de localisations télémétriques ponctuelles, nous avons déterminé que les localisations des aires utilisées en mer, la distance à partir de la colonie et la profondeur de l'eau ont varié significativement entre les années. En 1999 et 2000, les oiseaux marqués se trouvaient en moyenne à ~50 km au sud-ouest de l'île Triangle, dans des eaux d'une profondeur approximative de 1,400–1,800 m. Toutefois, en 2001, les oiseaux marqués se trouvaient en moyenne à ~80 km au nord-ouest de l'île Triangle, dans des eaux profondes d'environ 725 m. Intra-annuellement (i.e. entre des inventaires s'étalant sur plusieurs jours ou semaines), il n'y avait pas de changement directionnel à grande échelle concernant l'aire marine utilisée. La taille des aires marines utilisées (quantifiée en utilisant la méthode de Kernel [KHR]) variait entre les trois années d'environ 650 à 1,400 km^2 (50% KHR) et approximativement de 3,200 à 8,200 km^2 (95% KHR).

[3]E-mail: sean.boyd@ec.gc.ca
[4]Present address: 28-7251 Cariboo Drive, Burnaby, British Columbia V3N 4Y3, Canada.
[5]Present address: Yukon Land Use Planning Council, 201-307 Jarvis Street, Whitehorse, Yukon Y1A 2H3, Canada.
[6]Present address: Institute of Ocean Sciences, 9860 West Saanich Road, P.O. Box 6000, Sidney, British Columbia V8L 4B2, Canada.

Colonial-nesting seabirds are abundant in waters surrounding colonies during the breeding season and, as a result, are vulnerable to changes or disturbance to their local marine environment. Any endeavor to protect the waters surrounding seabird colonies must take into account the at-sea distributions of key species and how these distributions vary over time (Yen et al. 2004). Natural variability in oceanic conditions (Hay 1992; Ainley et al. 1996; Yen et al. 2004, 2005) can cause variation in the location and quantity of ephemeral prey (Vermeer et al. 1985, Obst et al. 1995, Davoren 2000, Kitaysky et al. 2000), and this can result in subsequent distributional shifts of foraging seabirds. In addition, the strength of the association between seabirds and their prey depends on the scale at which we integrate information (Logerwell and Hargreaves 1996, Parrish et al. 1998).

Triangle Island is home to 13 seabird species, including 55% of the world's population of Cassin's Auklets (*Ptychoramphus aleuticus*) (Rodway et al. 1992). The island is near the continental shelf-break, a transition zone where oceanic fronts and their subsequent influence on zooplankton populations attract dense concentrations of fish and seabirds (Hay 1992, Logerwell and Hargreaves 1996, Hunt 1997, Russell et al. 1999). It is not known how seabirds nesting at Triangle Island incorporate this transition zone into their marine area of use.

Quantifying at-sea patterns of distribution will be useful as a baseline against which to measure future changes resulting from some natural environmental change or anthropogenic disturbance. In turn, this will assist management action at the appropriate scale (Burger et al. 2004). One management action receiving attention on the Pacific coast in recent years has been the identification of marine areas of high conservation value to be considered for protection. The marine foraging area around the Scott Islands, which includes Triangle Island, will be part of this assessment. A key criterion, supported by the present study, is the need to be responsive to the natural variations in use by marine organisms when defining core areas of highest conservation value.

We conducted a three-year investigation to describe the size and location of the marine areas used by Cassin's Auklets (hereafter "auklets") breeding at Triangle Island. Our objectives were to delineate the at-sea distribution of these birds during the daytime and to document the amount of variation in their marine use areas within the chick-rearing period and across years.

Methods

Capture and transmitter attachment.—We captured 112 auklets on the western slopes of Triangle Island (50°52′N; 129°05′W; see Fig. 1) between 6 and 19 June in 1999 ($n = 39$), 23 May and 19 June in 2000 ($n = 35$), and 14 and 23 May in 2001 ($n = 38$). Captures occurred at night and were timed to coincide roughly with the midpoint of the 45-day chick-rearing period. Sixty-three adult birds were removed from burrows containing nestlings, and 49 were captured in stationary "pheasant" nets as they returned to the colony to deliver food-loads to nestlings.

Miniature VHF transmitters were used to mark the birds. We affixed the transmitters dorsally between the scapulars with subcutaneous anchors (model 394, Advanced Telemetry Systems, Holohil Systems, Carp, Ontario) using the protocol described in Newman et al. (1999), but without anesthetic and with epoxy instead of sutures to secure the device. The transmitters weighed 2.2 g and had an expected lifespan of 45 days.

Telemetry detections.—To confirm whether birds detected during aerial surveys were attending the colony, we used a remote recording system (Data Collection Computer [DCC] II, model D5041; Advanced Telemetry Systems) to monitor nocturnal attendance. The DCC was active nightly during the capture and survey periods in all years (14 June to 6 July 1999; 24 May to 7 July 2000; 25 May to 30 July 2001).

We conducted two sets of aerial telemetry surveys during the chick-rearing stage in 1999 (9–10 June and 23–24 June) and two sets in 2000 (31 May to 1 June and 15–16 June). The sets were approximately two weeks apart, and each consisted of several surveys conducted over consecutive days. One observer was present during these surveys. In 2001, we conducted only one set of surveys during the middle of the chick-rearing period (5–7 June). Two observers were present on the 2001 surveys, each scanning both sides of the aircraft simultaneously. The same primary observer (W.S.B.) was present in all three years. All surveys were flown in a DeHaviland Beaver on floats. Except for the first survey period in 1999, in which two H-antennae were used, all other surveys used two four-element yagi antennae mounted to the aircraft struts. Each survey lasted 4–5 h, including transit time to and from Port Hardy on the northeast coast of Vancouver Island.

The first day of each survey set involved circling Triangle Island out to ~10 km offshore. Subsequent surveys involved large transect grids to the west of the island (Fig. 1). Observations from shipboard surveys conducted in the 1980s and 1990s suggested that most of the auklets were concentrated in this area (Environment Canada unpubl. data). Although we reached Triangle Island or the transect grids from Port Hardy via many different routes, we detected only a few transmitters on the island, in adjacent waters, or to the east of the island. Hence, we are confident that most of the radiomarked birds were to the west of Triangle Island, where we focused our telemetry effort.

In contrast to Adams et al. (2004), we did not attempt to pinpoint the exact location of each transmitter by circling at low altitude. Such a procedure would have consumed too much fuel and time. Instead, we flew transects at ~3,000 m primarily in east–west directions (Fig. 1). Transects were initially ~15 km apart and then reduced to 7–8 km apart on subsequent surveys, to concentrate survey effort in the area where most birds were detected.

Each time a transmitter was detected, its signal strength (scored from one to five, with five being the strongest signal) and direction (left or right side of aircraft with respect to flight path) were recorded, along with the latitude and longitude of the aircraft using a global positioning system (GPS). On average, each radiomarked bird was detected seven times during each survey (range: 1–30 detections). All detections for each radiomarked bird were used to determine the most likely or "inferred" location during each survey (see details below). The spatial coverage of our aerial surveys was similar from year to year, so we are confident that the distributions we describe are accurate and not attributable to some sampling artifact.

To evaluate the accuracy of our at-sea positioning protocol, we compared our inferred locations derived from the aerial surveys with the positions of (1) radiomarked birds in burrows at Triangle
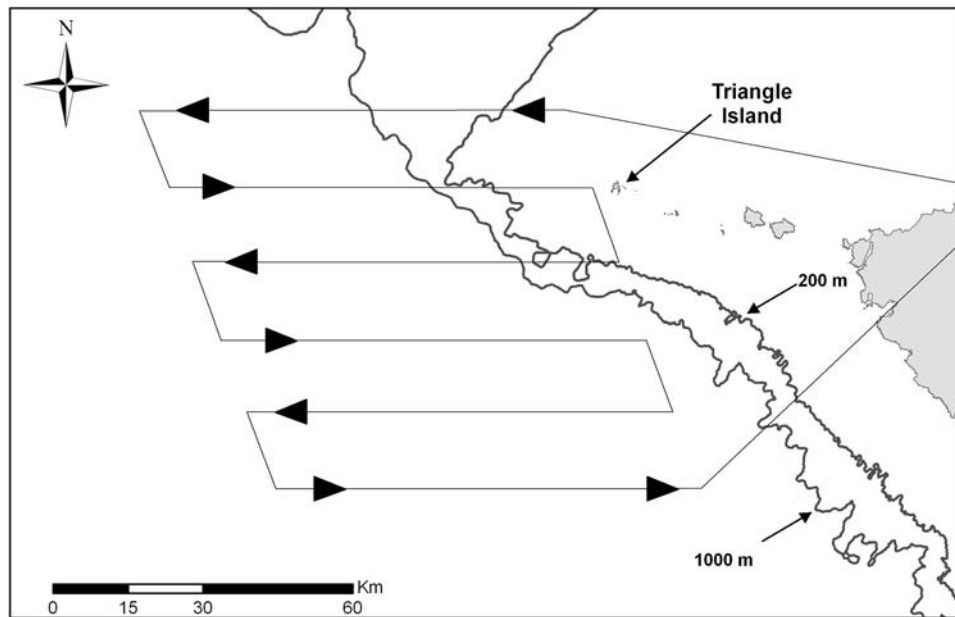
Fig. 1. An example of a high-altitude survey grid for locating radiomarked Cassin's Auklets at Triangle Island during the chick-rearing period (east–west transects, ~15 km apart, 15 June 2000). The "200 m" and "1000 m" markings refer to isobaths.

Island and (2) test transmitters deployed on a buoy off the west side of the island.

Inferring telemetry locations and mapping marine distributions.—British Columbia Albers projection was used for mapping and analysis with ARCVIEW GIS software, version 3.2 (ESRI, Redlands, California). For each survey, all detections for each radiomarked bird were plotted along with aircraft location and transmitter signal strength and direction (Fig. 2). The resulting
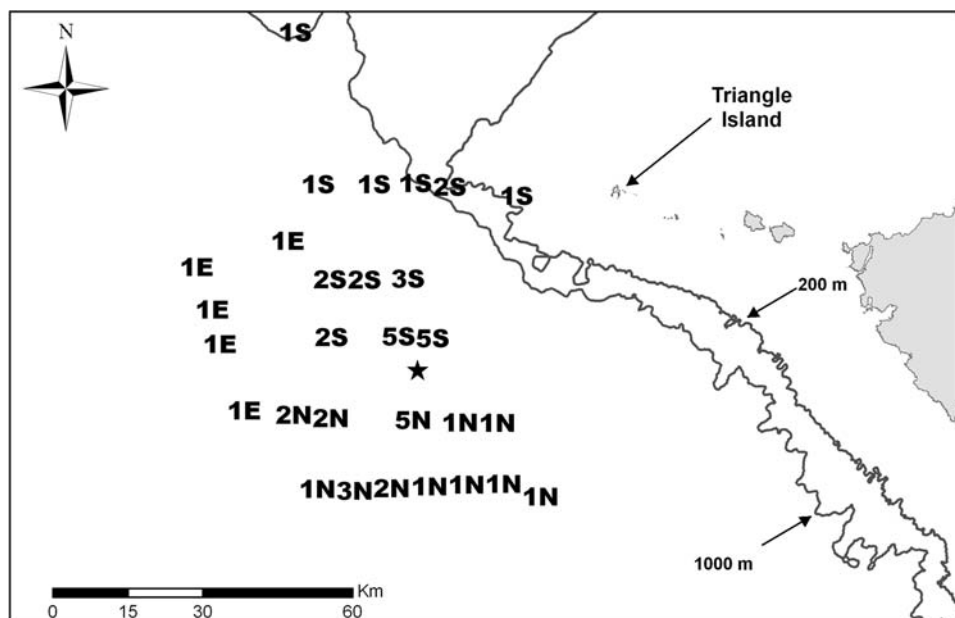

Fig. 2. An example of location data recorded for one Cassin's Auklet radiomarked at Triangle Island and detected during the chick-rearing period (frequency 164.133; 23 June 1999). The inferred location is indicated by the star, the number indicates signal strength of the transmitter (1–5, maximum = 5), and the letter indicates direction of the radiomarked bird in relation to aircraft location (S = south, etc).
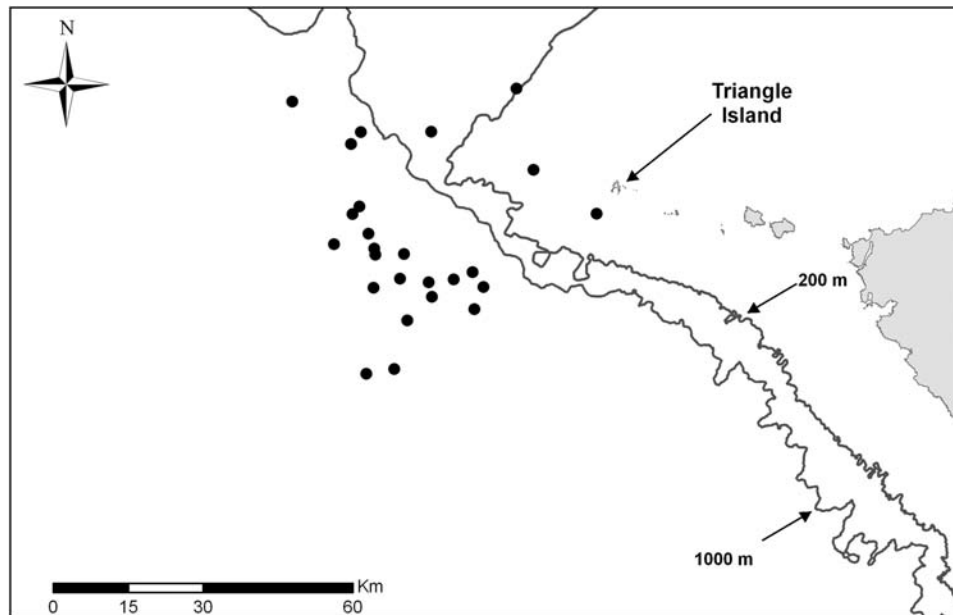
FIG. 3. An example showing the at-sea locations of all radiomarked Cassin's Auklets detected during a survey on 15 June 2000. Auklets were radiomarked at Triangle Island and telemetry was conducted during the chick-rearing period. Each dot represents the inferred location of one radiomarked individual (see text for details).

pattern of signal strengths and directions was used to infer the most likely location for each bird (Fig. 2), and these locations were then plotted for all birds detected during each survey (Fig. 3). We assumed that the birds did not move during each survey.

The inferred locations were used to map (1) distance from Triangle Island and water depth for individuals and (2) marine use area (see below). For interannual comparisons, we used only one inferred location per individual per year; that is, if an individual was detected on more than one survey within a year, we randomly chose a single inferred location for that individual.

We used the ANIMAL MOVEMENT extension in ARCVIEW to compute Kernel home ranges (KHR; Hooge and Eichenlaub 1997), with a nonparametric kernel-density estimator and a fixed kernel method (Seaman and Powell 1996, Seaman et al. 1998, Kenward 2001). The KHR method uses location data to extrapolate and smooth the probability of detecting a radiomarked individual within an area, thereby creating a "home range" for that individual. We modified this method to generate 50% and 95% KHRs by pooling the inferred locations (see Fig. 3) from all radiomarked individuals ("colony home range" method; cf. Adams et al. 2004). In simple terms, these KHRs outline areas in which marked individuals are most likely to spend 50% and 95% of their time, respectively. We used 50% KHR to assess variation in marine use area across surveys, and both 95% and 50% KHR to assess variation in marine use area across years. We used ARCVIEW to calculate the overlap (percentage of shared area) of KHRs between surveys and years. On average, 24 radiomarked birds (range: 16–32) were available to plot KHRs for each survey. Annual KHRs comprised 30, 33, and 28 individuals in 1999, 2000, and 2001, respectively. Differences in sample sizes are attributable to the fact that not all transmitters were detected during each

survey but annual KHRs used all transmitters detected each year.

Adams et al. (2004) used the 95% KHR to describe overall colony "activity area" and the 50% KHR to describe "core foraging areas." The marine use areas we describe here do not necessarily correspond to foraging areas (i.e., we cannot confirm that foraging occurred at inferred telemetry locations), though they may be similar.

RESULTS

Approximately 70% (78 of 112) of the radiomarked auklets in the present study attended the colony on a daily or twice-daily basis (Table 1). The remaining birds either attended at irregular intervals with long periods of absence from the colony (9%), were detected at sea but not at the colony (10%; 7% of which were confirmed to have abandoned the colony), or were not detected at all following transmitter attachment (11%).

In 1999, the distance (mean $\pm$ SE) from the true to inferred locations of five transmitters at the colony was 4.5 $\pm$ 2.0 km, with a maximum distance of 6.8 km. Four of these transmitters were detected only once, so we expect that the inferred locations for transmitters detected several times during a survey would be more accurately predicted. In support of this, the average distance from the true to inferred location for the two test transmitters ($n =$ 15 and 27 detections, respectively) on the floating buoy in 2000 was 3.3 $\pm$ 0.5 km, despite the buoy being positioned just outside the primary aerial-survey grid. Also in 2000, the average distance between true and inferred locations for two radiomarked birds in burrows at the colony was 2.7 $\pm$ 0.2 km. On the basis of the above,

Table 1. Number of Cassin's Auklets radiomarked at Triangle Island each year (1999–2001) and detection rates at sea and at the colony.

Year	Number of radiomarked auklets	Total detected at sea	Regular colony attendance	Irregular colony attendance	Detected at sea only (abandoned colony)	Not detected at sea or colony
1999	39	29 (74%)	26 (67%)	1	5 (2)	7
2000	35	31 (88%)	27 (77%)	0	6 (6)	2
2001	38	28 (73%)	25 (60%)	7	2 (2)	4
Total	112	88 (79%)	78 (70%)	10 (9%)	11 (10%)	13 (11%)

we estimate that each inferred location was within 3 km of its true location, which equates to a small area in relation to the size of the ocean area surveyed.

For radiomarked birds attending the colony versus those not detected at the colony (or having abandoned the colony), there was no significant difference in distance from Triangle Island (analysis of variance [ANOVA], $F < 0.001$, df = 2 and 210, $P = 0.97$) or water depth ($F < 0.001$, df = 2 and 210, $P = 0.99$) across the three years. Thus, for further analysis of distance and depth from colony, we included all radiomarked birds.

We recorded 1,655 detections during nine aerial surveys conducted from 1999 to 2001. Of the 112 radiomarked birds, 88 (79%) were detected at sea during at least one survey (Table 1). On average, over the three years, inferred locations were 51.9 ± 5.0 km (range: 3.5–113.3 km) from Triangle Island. Average 50% and 95% KHRs were 1,010 and 5,250 km^2, respectively.

In 1999, radiomarked birds were at the same distance (ANOVA with Tukey's pairwise comparisons, $F = 0.56$, df = 2 and 57, $P = 0.57$) and depth ($F = 1.12$, df = 2 and 57, $P = 0.33$) during three surveys conducted over a two-week period (10, 23, and 24 June; Table 2). This was not the case in 2000, when distance ($F = 3.86$, df = 3 and 97, $P = 0.012$) and depth ($F = 3.7$, df = 3 and 97, $P = 0.014$) differed significantly across four surveys conducted over a two-week period (31 May; and 1, 15, and 16 June). Likewise, in 2001, radiomarked birds were detected at significantly different distances (two-sample t-test, $T = -2.99$, df = 42, $P = 0.005$) and

water depths ($T = -2.48$, df = 33, $P = 0.018$) between surveys conducted over two consecutive days (6 and 7 June).

In 1999, average 50% KHR per survey was 34.9 km^2 (Table 2). Across the two surveys with the most comparable aerial coverage (10 and 23 June 1999), the 50% KHRs overlapped by 12.8% (Fig. 4A). In 2000, average 50% KHR per survey was 27.1 km^2. The 50% KHRs calculated from pairs of surveys conducted over consecutive days (31 May and 1 June 2000; 15 and 16 June 2000) overlapped more (16% and 32%, respectively) than those from surveys separated by two weeks (1 and 15 June 2000; 0.1% overlap); in other words, the assemblage of radiomarked auklets moved more across weeks than days (Fig. 4B). In 2001, average 50% KHR per survey was 44.8 km^2. We did not assess core foraging overlap between surveys in 2001 because of insufficient overlap of coverage.

Across years, the size of the 50% and 95% KHRs varied substantially (Table 2 and Fig. 5). Both 50% and 95% KHRs were primarily southwest of the colony in 1999 and 2000 but northwest of the colony in 2001. Overlap for 50% KHR was 16% between 1999 and 2000, 0% between 2000 and 2001, and 0% between 1999 and 2001 (Fig. 5A). Overlap for 95% KHR was 23.3% between 1999 and 2000, 14.0% between 2000 and 2001, and 13.5% between 1999 and 2001 (Fig. 5B). In addition, mean distance from Triangle Island and water depth differed across years (ANOVA with Tukey's pairwise comparisons: for depth, $F = 23.35$, df = 2 and 85, $P < 0.001$; and for distance, $F = 15.36$, df = 2 and 85, $P < 0.001$; Table 2).

Table 2. Distance from colony and ocean depth and marine use areas (95% and 50% KHRs) for Cassin's Auklets radiomarked at Triangle Island, 1999–2001.

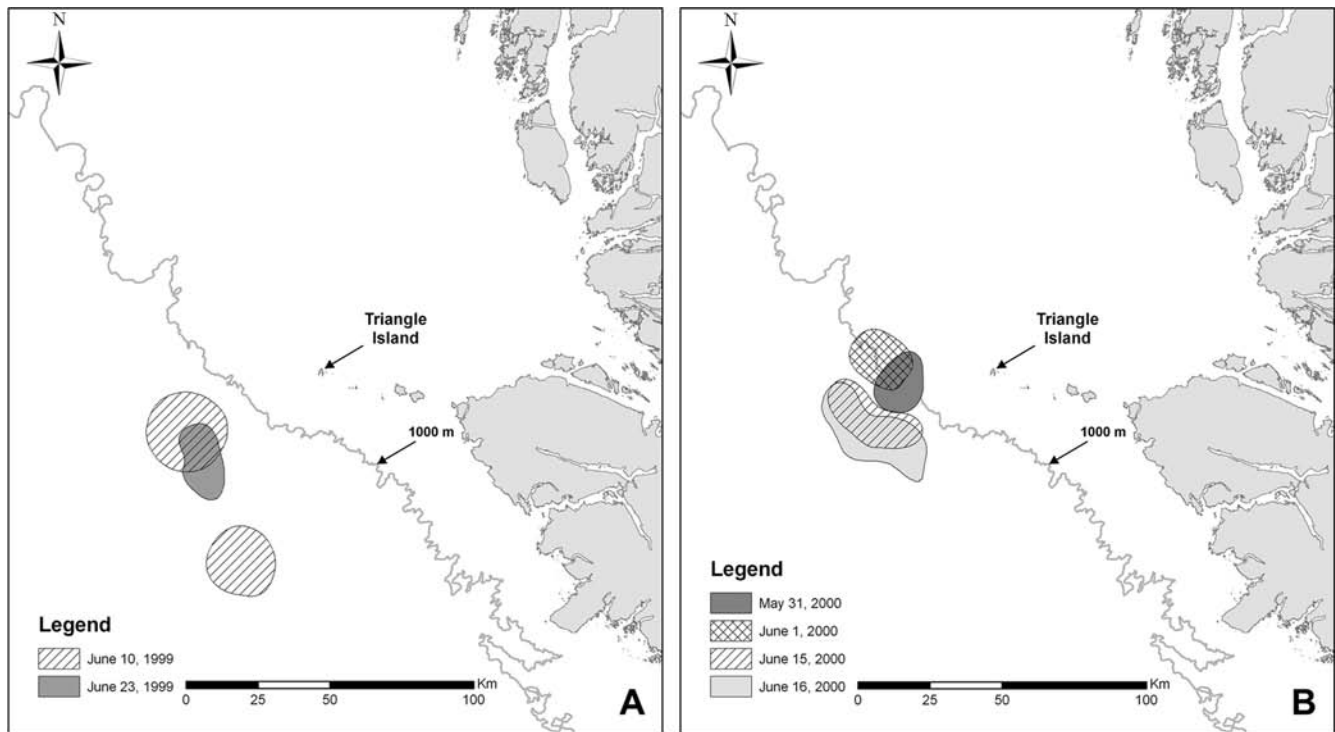| Year	Date of survey	Birds (n)	Distance (km) (mean ± SE)	Range (km)	Depth (m) (mean ± SE)	Range (m)	50% KHR (km^2)	95% KHR (km^2)
1999	10 June	16	58.9 ± 5.1		1839.4 ± 122.7		68.6	
	23 June	24	54.0 ± 3.1		1827.5 ± 108.7		20.1	
	24 June	20	57.8 ± 2.3		2011.3 ± 46.1		16.0	
Annual		30	54.5 ± 2.8	8.9–79.3	1843.7 ± 92.3	93–2,153	646.1	4,352.0
2000	31 May	16	34.6 ± 1.7		1230.4 ± 177.0		17.7	
	1 June	32	39.7 ± 2.1		1196.6 ± 138.2		21.0	
	15 June	25	44.7 ± 2.7		1670.8 ± 135.2		28.6	
	16 June	28	46.0 ± 2.5		1690.9 ± 126.3		41.0	
Annual		33	41.0 ± 2.5	3.5–62.6	1373.0 ± 141.0	67–2,136	757.9	3,192.6
2001	6 June	25	56.4 ± 5.1		489.0 ± 79.6		23.9	
	7 June	22	80.1 ± 6.2		889.0 ± 140.0		65.6	
Annual		28	69.8 ± 5.3	16.2–113.3	724.1 ± 99.2	113–1,841	1,399.6	8,203.9

FIG. 4. Fifty-percent kernel home ranges for radiomarked Cassin's Auklets during the chick-rearing period (A) in 1999 (10 and 23 June) and (B) in 2000 (31 May; and 1, 15, and 16 June).
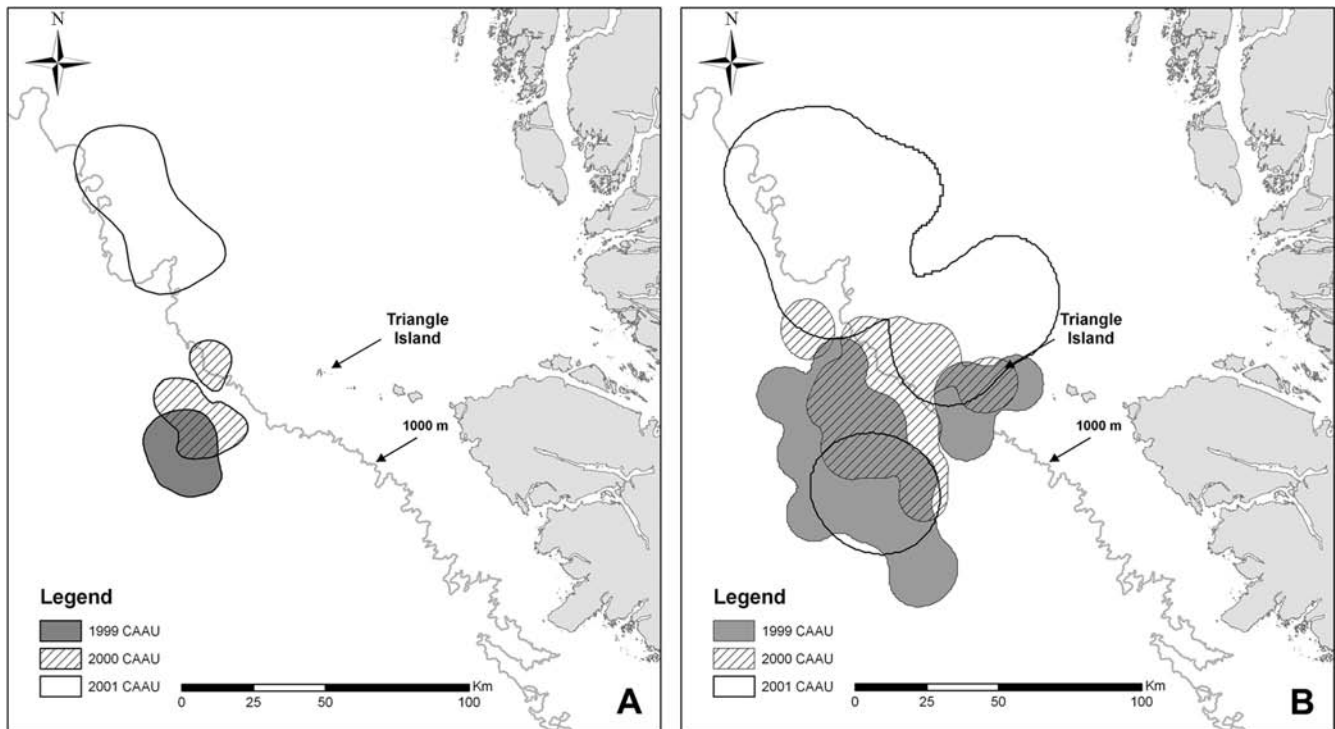

FIG. 5. (A) Fifty-percent kernel home ranges and (B) 95% kernel home ranges for radiomarked Cassin's Auklets during the chick-rearing period across three years, 1999–2001.

Discussion

Areas of marine activity.—Of the 112 auklets radiomarked at Triangle Island from 1999 to 2001, 9% attended the colony irregularly, 10% were detected at sea but not at the colony, and 11% were not detected following transmitter attachment. Irregular attendance behavior may reflect a handling or transmitter effect (Söhle et al. 2000, Hamel et al. 2004); changes in availability of prey, which may be patchily distributed, unpredictable, or in short supply (Zador and Piatt 1999, Kitaysky et al. 2000, Fraser et al. 2002); or weather events (Piatt et al. 1990, Weidinger 1996). Hamel et al. (2004) found that patterns of colony attendance and chick provisioning by Common Murres (*Uria aalge*) differed between birds with and without radiotransmitters. Our undetected auklets may have experienced transmitter failure or their transmitters may have fallen off, the birds may have died, or they may have departed the study area completely. The estimated failure rate of the same ATS transmitters attached to Marbled Murrelets (*Brachyramphus marmoratus*) in Desolation Sound, British Columbia, in 2000 and 2001 was 5–6% (Centre for Wildlife Ecology, Simon Fraser University, unpubl. data). The degree to which transmitters influenced the at-sea distribution and colony attendance patterns of our radiomarked auklets is unknown. We have no colony attendance data for unmarked birds to compare, and it is impossible to locate unmarked birds on the open ocean.

We also do not know whether the marine use areas described here correspond to areas where adults are capturing food for their chicks. This topic requires further investigation (cf. Mehlum 2001, Weimerskirch et al. 2003, Wilson et al. 2004). Although the KHRs we describe no doubt encompass resting areas, resting is likely intermittent between bouts of diving for prey (Schwemmer and Garthe 2005). In addition, the KHRs do not include Triangle Island as a starting point but it is reasonable to assume that travel corridors between the colony and marine use areas constitute part of the ocean territory used by the auklets.

Although the number of auklets detected at sea each year did not differ markedly (73–88% of radiomarked birds; Table 1), the 50% KHRs varied across the three years of our study (from approximately 650 to 1,400 km^2), as did the 95% KHRs (from approximately 3,200 to 8,200 km^2). These variations cannot be explained by differential coverage because the same initial grid was flown each year, followed by subsequent transects until no new radiomarked birds were detected.

We documented a significant shift in marine use area across years, particularly in 2001, when the 50% KHR did not overlap at all and the 95% KHR overlapped those of the two previous years by only ~14%. In 2001, most radiomarked birds were concentrated ~80 km northwest of Triangle Island. This is a substantial shift from the marine distributions in both 1999 and 2000, when the auklets were consistently centered ~50 km southwest of Triangle Island, with an interannual overlap in 95% KHR of 23% and an overlap in 50% KHR of 16%. This interannual shift from south to north was corroborated by the marine detections of the same (re-)marked individual found southwest of Triangle Island in 1999 but northwest in 2001; and the consistency of another (re-)marked individual found southwest of Triangle Island in both 1999 and 2000. Also, in contrast to 1999 and 2000, when most of the

radiomarked auklets were seaward of the 1,000 m isobath and in waters roughly 1,400–1,800 m deep, only a few birds were seaward of this isobath in 2001; the remaining birds were found in more shallow water averaging ~725 m depth.

The changes in KHR size and location suggest that oceanic factors affecting the distribution or availability of key zooplankton prey populations, particularly *Neocalanus cristatus* and *Tysanoesa* spp. (Bertram et al. 2001, Hedd et al. 2002), likely changed between 2000 and 2001. In a similar study covering the same study years (1999–2001), Adams et al. (2004) found radiomarked auklets within 30 km from two colonies, because of the proximity of deep water canyons in the California Current System where their main prey are predictably located. They found that 50% KHRs were spatially consistent among years for each of their two study colonies, overlapping by 30–67% from 1999 to 2001. However, it is interesting to note that their overall distribution of locations in 2001 shifted slightly (10 km) northwestward compared with 1999 and 2000. Studies in California (Briggs et al. 1987, Ainley et al. 1996, Adams et al. 2004), Alaska (Sanger 1987), and British Columbia (Vermeer et al. 1985) reported that auklets foraged near the continental shelf break during the breeding season, but with annual variation around isobaths. Hence, variation in oceanic processes (e.g., fronts and upwelling) influences the spatial aggregation of prey and, consequently, foraging areas are expected to vary annually in agreement with these marine influences (Hay 1992, Logerwell and Hargreaves 1996, Hunt 1997, Russell et al. 1999, Lilliendahl et al. 2003, Adams et al. 2004).

The present study is the first to describe the marine use area of Cassin's Auklets nesting at Triangle Island, the largest breeding colony of this species in the world. Our results demonstrate that the at-sea distribution of this species can vary substantially across years. One direct use of our data would be to help with the delineation of a marine area of conservation interest around Triangle Island and, more broadly, the Scott Island Group. Marine conservation areas are typically used where species concentrate in high numbers or where they have strong habitat-specific associations (Begg et al. 2005, Gerber et al. 2005, Kaiser 2005). If the primary goal is to maintain the integrity of the local waters to support seabird populations, variations in their spatial and temporal distributions must be taken into account. Such an exercise requires multiple years of data collection based on an empirical assessment of the distribution of colony inhabitants, as we have done here. For Cassin's Auklets, this may mean that the area of conservation interest should extend to the outer limits of the 95% KHRs to capture the range of natural variability in activity patterns observed across years. The distribution patterns of other seabird species nesting at Triangle Island or during other stages of the annual cycle (e.g., incubation) may suggest that different and perhaps even larger areas should be considered for protection.

Literature Cited

Adams, J., J. Y. Takekawa, and H. R. Carter. 2004. Foraging distance and home range of Cassin's Auklets nesting at two colonies in the California Channel Islands. Condor 106:618–637.

Ainley, D. G., L. B. Spear, and S. G. Allen. 1996. Variation in the diet of Cassin's Auklet reveals spatial, seasonal, and decadal occurrence patterns of euphausiids off California, USA. Marine Ecology Progress Series 137:1–10.

Begg, G. A., B. D. Mapstone, A. J. Williams, S. Adams, C. R. Davies, and D. C. Lou. 2005. Multivariate life-history indices of exploited coral reef fish populations used to measure the performance of no-take zones in a marine protected area. Canadian Journal of Fisheries and Aquatic Sciences 62:679–692.

Bertram, D. F., D. L. Mackas, and S. M. McKinnell. 2001. The seasonal cycle revisited: Interannual variation and ecosystem consequences. Progress in Oceanography 49:283–307.

Briggs, K. T., W. B. Tyler, D. B. Lewis, and D. R. Carlson. 1987. Bird communities at sea off California: 1975 to 1983. Studies in Avian Biology, no. 11.

Burger, A. E., C. L. Hitchcock, and G. K. Davoren. 2004. Spatial aggregations of seabirds and their prey on the continental shelf off SW Vancouver Island. Marine Ecology Progress Series 283:279–292.

Davoren, G. K. 2000. Variability in foraging in response to changing prey distributions in Rhinoceros Auklets. Marine Ecology Progress Series 198:283–291.

Fraser, G. S., I. L. Jones, and F. M. Hunter. 2002. Male–female differences in parental care in monogamous Crested Auklets. Condor 104:413–423.

Gerber, L. R., S. S. Heppell, F. Ballantyne, and E. Sala. 2005. The role of dispersal and demography in determining the efficacy of marine reserves. Canadian Journal of Fisheries and Aquatic Sciences 62:863–871.

Hamel, N. J., J. K. Parrish, and L. L. Conquest. 2004. Effects of tagging on behavior, provisioning, and reproduction in the Common Murre (*Uria aalge*), a diving seabird. Auk 121:1161–1171.

Hay, R. B. 1992. The oceanic habitats of seabirds: Their zonal distribution off Vancouver Island, British Columbia, Canada. Journal of Biogeography 19:67–85.

Hedd, A., J. L. Ryder, L. L. Cowen, and D. F. Bertram. 2002. Inter-annual variation in the diet, provisioning and growth of Cassin's Auklet at Triangle Island, British Columbia: Responses to variation in ocean climate. Marine Ecology Progress Series 229:221–232.

Hooge, P. N., and B. Eichenlaub. 1997. ANIMAL MOVEMENT extension to ARCVIEW, version 1.1. U.S. Geological Survey, Alaska Biological Science Center, Anchorage.

Hunt, G. L., Jr. 1997. Physics, zooplankton, and the distribution of Least Auklets in the Bering Sea—A review. ICES Journal of Marine Science 54:600–607.

Kaiser, M. J. 2005. Are marine protected areas a red herring or fisheries panacea? Canadian Journal of Fisheries and Aquatic Sciences 62:1194–1199.

Kenward, R. E. 2001. A Manual for Wildlife Radio Tagging. Academic Press, London.

Kitaysky, A. S., G. L. Hunt, Jr., E. N. Flint, M. A. Rubega, and M. B. Decker. 2000. Resource allocation in breeding seabirds: Responses to fluctuations in their food supply. Marine Ecology Progress Series 206:283–296.

Lilliendahl, K., J. Solmundsson, G. A. Gudmundsson, and L. Taylor. 2003. Can surveillance radar be used to monitor the foraging distribution of colonially breeding alcids? Condor 105:145–150.

Logerwell, E. A., and N. B. Hargreaves. 1996. The distribution of sea birds relative to their fish prey off Vancouver Island: Opposing results at large and small spatial scales. Fisheries Oceanography 5:163–175.

Mehlum, F. 2001. Crustaceans in the diet of adult Common and Brünnich's guillemots *Uria aalge* and *U. lomvia* in the Barents Sea during the breeding period. Marine Ornithology 29:19–22.

Newman, S. H., J. Y. Takekawa, D. L. Whitworth, and E. E. Burkett. 1999. Subcutaneous anchor attachment increases retention of radio transmitters on Xantus' and Marbled murrelets. Journal of Field Ornithology 70:520–534.

Obst, B. S., R. W. Russell, G. L. Hunt, Jr., Z. A. Eppley, and N. M. Harrison. 1995. Foraging radii and energetics of Least Auklets (*Aethia pusilla*) breeding on three Bering Sea islands. Physiological Zoology 68:647–672.

Parrish, J. K., N. Lemberg, and L. South-Oryshchyn. 1998. Effects of colony location and nekton abundance on the at-sea distribution of four seabird species. Fisheries Oceanography 7:126–135.

Piatt, J. F., B. D. Roberts, and S. A. Hatch. 1990. Colony attendance and population monitoring of Least and Crested auklets on St. Lawrence Island, Alaska. Condor 92:97–106.

Rodway, M. S., M. J. F. Lemon, and K. R. Summers. 1992. Seabird breeding populations in the Scott Islands on the west coast of Vancouver Island, 1982–89. Pages 52–59 *in* The Ecology, Status, and Conservation of Marine and Shoreline Birds on the West Coast of Vancouver Island (K. Vermeer, R. W. Butler, and K. H. Morgan, Eds.). Canadian Wildlife Service, Ottawa, Occasional Paper, no. 75.

Russell, R. W., N. M. Harrison, and G. L. Hunt, Jr. 1999. Foraging at a front: Hydrography, zooplankton, and avian planktivory in the northern Bering Sea. Marine Ecology Progress Series 182:77–93.

Sanger, G. A. 1987. Trophic levels and trophic relationships of seabirds in the Gulf of Alaska. Pages 229–257 *in* Seabirds: Feeding Ecology and Role in Marine Ecosystems (J. P. Croxall, Ed.). Cambridge University Press, Cambridge, United Kingdom.

Schwemmer, P., and S. Garthe. 2005. At-sea distribution and behavior of a surface feeding seabird, the Lesser Black-backed Gull *Larus fuscus*, and its association with different prey. Marine Ecology Progress Series 285:245–258.

Seaman, D. E., B. Griffith, and R. A. Powell. 1998. KERNELHR: A program for estimating animal home ranges. Wildlife Society Bulletin 26:95–100.

Seaman, D. E., and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075–2085.

Söhle, I. S., H. Moller, D. Fletcher, and C. J. R. Robertson. 2000. Telemetry reduces colony attendance by Sooty Shearwaters (*Puffinus griseus*). New Zealand Journal of Zoology 27:367–373.

Vermeer, K., J. D. Fulton, and S. G. Sealy. 1985. Differential use of zooplankton prey by Ancient Murrelets and Cassin's Auklets in the Queen Charlotte Islands. Journal of Plankton Research 7:443–459.

Weidinger, K. 1996. Effects of weather on the cyclic patterns of colony attendance in the Cape Petrel (*Daption capense*). Polar Biology 16:339–344.

Weimerskirch, H., A. Ancel, M. Caloin, A. Zahariev, J. Spagiari, M. Kersten, and O. Chastel. 2003. Foraging efficiency and adjustment of energy expenditure in a pelagic seabird provisioning its chick. Journal of Animal Ecology 72:500–508.

Wilson, L. J., F. Danut, and S. Wanless. 2004. Self-feeding and chick provisioning diet differ in the Common Guillemot *Uria aalge*. Ardea 92:197–207.

Yen, P. P. W., W. J. Sydeman, and K. D. Hyrenbach. 2004. Marine bird and cetacean associations with bathymetric habitats and shallow-water topographies: Implications for trophic transfer and conservation. Journal of Marine Systems 50:79–99.

Yen, P. P. W., W. J. Sydeman, K. H. Morgan, and F. A. Whitney. 2005. Top predator distribution and abundance across the eastern Gulf of Alaska: Temporal variability and ocean habitat associations. Deep-Sea Research II 52:799–822.

Zador, S. G., and J. F. Piatt. 1999. Time-budgets of Common Murres at a declining and increasing colony in Alaska. Condor 101:149–152.

Associate Editor: A. E. Burger