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COEXISTENCE AND SPATIAL DISTRIBUTIONS OF MARBLED MURRELETS (*BRACHYRAMPHUS MARMORATUS*) AND OTHER ALCIDS OFF SOUTHWEST VANCOUVER ISLAND, BRITISH COLUMBIA

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Abstract.—Niche overlap and resource partitioning have seldom been investigated in the marine habitats of seabirds but are obvious determinants of community and population status. We investigated interspecific differences in densities and spatial aggregations of seabirds during summer (June–August) off southwest Vancouver Island, British Columbia. Two 300-m-wide parallel transects were sampled along 66.6 km of shoreline in 1993–1996, centered 200 m and 600 m from shore. Analysis focused on the threatened Marbled Murrelet (*Brachyramphus marmoratus*) and three other fish-eating alcids. Densities of Marbled Murrelets were among the highest reported at sea in the species' range; they were concentrated close to shore (>75% within 0.6 km and virtually all within 2.0 km of shore), usually in water <20 m deep, and showed strong fidelity to certain sectors along the coast from year to year. Common Murres (*Uria aalge*) and Rhinoceros Auklets (*Cerorhinca monocerata*) were not as closely associated with nearshore habitat as Marbled Murrelets, and their longshore distribution also differed from that of the latter. Neighbor-K analysis showed that Marbled Murrelets were usually segregated from Common Murres and, to a lesser extent, from Rhinoceros Auklets, but the latter two species were usually aggregated together. Marbled Murrelets also left the area after breeding, whereas numbers of Common Murres and Rhinoceros Auklets increased from June through August. Pigeon Guillemots (*Cepphus columba*) showed variable distributions and no consistent associations with other alcids. Marine distributions of Marbled Murrelets were markedly different from those of other fish-eating alcids, and we discuss this in relation to possible interference competition from the larger Common Murres and Rhinoceros Auklets. *Received 14 October 2006, accepted 28 April 2007.*

Key words: Alcidae, *Brachyramphus marmoratus*, *Cepphus columba*, *Cerorhinca monocerata*, Marbled Murrelet, marine habitats, resource partitioning, spatial distribution, *Uria aalge.*

Coexistence et répartitions spatiales de *Brachyramphus marmoratus* et autres alcidés au sud-ouest de l'île de Vancouver, en Colombie Britannique

Résumé.—Le chevauchement des niches et le partage des ressources ont rarement été étudiés dans les habitats marins des oiseaux de mer, bien qu'ils soient des déterminants certains du statut de la communauté et de la population. Nous avons étudié les différences interspécifiques des densités et des agrégations spatiales d'oiseaux de mer en été (juin–août) au sud-ouest de l'île de Vancouver, en Colombie Britannique. Deux transects parallèles, larges de 300 m et respectivement centrés à 200 m et 600 m du rivage, ont été échantillonnés le long de 66,6 km de rivage en 1993–1996. L'analyse portait sur *Brachyramphus marmoratus*, une espèce menacée, et sur trois autres alcidés piscivores. Les densités de *B. marmoratus* étaient parmi les plus élevées rapportées en mer dans les limites de répartition de l'espèce. Ces oiseaux se concentraient à proximité du rivage (>75% à moins de 0,6 km et pratiquement tous à moins de 2,0 km du rivage), où la profondeur de l'eau était habituellement <20 m, et présentaient une forte fidélité à certains secteurs le long de la côte d'une année à l'autre. *Uria aalge* et *Cerorhinca monocerata* n'étaient pas aussi étroitement associés à l'habitat près du rivage que *B. marmoratus* et leur répartition littorale était aussi différente de celle de ce dernier. Une analyse de groupement des K plus proches voisins (Neighbor-K) a démontré que *B. marmoratus* était habituellement isolé de *U. aalge* et, dans une moindre mesure,

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de *C. monoerata*. Cependant, ces deux dernières espèces étaient habituellement ensemble. *B. marmoratus* a quitté le secteur après la période de reproduction, alors que les abondances de *U. aalge* et *C. monocerata* ont augmenté de juin à août. *Cepphus columba* présentait des répartitions variables, sans association constante avec les autres alcidés. Les répartitions en mer de *B. marmoratus* étaient remarquablement différentes de celles des autres alcidés piscivores et nous discutons de ceci relativement à une possible compétition d'interférence avec des espèces de plus grande taille comme *U. aalge* et *C. monocerata*.

Inter- and intraspecific behavioral interactions among birds foraging at sea are often difficult to identify and quantify but could have important effects on the densities and distributions of these birds (Shealer and Burger 1993, Lewis et al. 2001, Shealer 2002). It is usually easier to recognize positive, aggregative behavior, such as attraction to mixed-species feeding flocks (Porter and Sealy 1981, 1982) than negative or avoidance behavior (Hoffman et al. 1981, Maniscalco et al. 2001). Consequently, few studies have documented differences in fine-scale spatial distributions or behavioral interactions among seabird species that might be interpreted as avoidance or interference competition (Piatt 1990), though intraspecific interference competition has been inferred from analyses of at-sea distributions of seabirds (Logerwell et al. 1998, Lewis et al. 2001, Ainley et al. 2003, Davoren et al. 2003).

Here, we examine marine distributions of four species of sympatric piscivorous alcids in the nearshore waters off southwest Vancouver Island, where these birds have high densities during the summer breeding season. In particular, we focus on densities, spatial distribution, and possible interspecific interactions of the Marbled Murrelet (*Brachyramphus marmoratus*; hereafter "murrelet"), a species listed as threatened in Canada and in Washington, Oregon, and California (Burger 2002, McShane et al. 2004). The other piscivorous alcids commonly found in the study area are Common Murres (*Uria aalge*; hereafter "murres"), Rhinoceros Auklets (*Cerorhinca monocerata*; hereafter "auklets"), and Pigeon Guillemots (*Cepphus columba*; hereafter "guillemots").

In addition to examining concepts of coexistence within a guild of piscivorous birds, our study contributes to understanding factors that affect the spatial distribution of murrelets compared with other sympatric alcids. This is important for three reasons. First, the difficulties of monitoring breeding success, diets, and population parameters of murrelets have led biologists to rely on comparative data from related alcid species (e.g., De Santo and Nelson 1995, Beissinger and Nur 1997) and to use these species as proxies for predicting likely effects on murrelets of major events such as El Niño and global climate change (McShane et al. 2004). It is important, therefore, to know how closely the marine niches of murrelets match those of other species likely to be used as proxies in such situations. Second, interspecific competition with other, larger piscivorous alcids may affect the foraging success, marine distributions, and population dynamics of murrelets. Size-related interference competition at sea has seldom been investigated in seabirds but was suggested between Atlantic Puffins (*Fratercula arctica*) and larger murres off Newfoundland (Piatt 1990). There is circumstantial evidence (Chilton and Sealy 1987, Mahon et al. 1992) that interference might cause murrelets to avoid mixed-species aggregations, in which piscivorous seabirds frequently feed in the northeast Pacific (Hoffman et al. 1981; Porter and Sealy 1981, 1982; Maniscalco et al. 2001). Finally, understanding spatial distribution and the consistency of site use is important for management and contingency planning for the threatened murrelet, which is susceptible to oil spills, fisheries bycatch, disturbance from boat traffic, and conflicts with aquaculture (Ralph et al. 1995, Burger 2002, Piatt et al. 2006).

Methods

Study area and transect routes.—We conducted vessel surveys along fixed-strip transects covering 66.6 km of coast between Cape Beale (48°47.15′N, 125°13.00′W) and Owen Point (48°32.62′N, 124°29.83′W) (Fig. 1). Most of this coastline, and waters within the 20-m-depth isobath, fall within the West Coast Trail portion of Pacific Rim National Park Reserve. We used two parallel longshore transect routes, covering an "inner zone" (transect midline running ~200 m offshore) and an "outer zone" (midline 600 m offshore). The outer transect was parallel to the first but far enough apart to avoid resampling the inner zone. The ship's radar was used to maintain a relatively constant distance from shore. Both transect strips were 300 m wide (150 m on either side of the vessel). Our protocol was to sample the inner zone on the outward leg of the voyage (usually starting at Cape Beale) and the outer zone on the homeward leg.

Surveys were made from June through August, during the time that all four alcid species were breeding, in 1993 (1 survey), 1994 (5), 1995 (5), and 1996 (2). Most surveys covered the entire inner and outer transects, but a few were truncated when the weather deteriorated.

Bird counts.—All seabird and sea duck species were counted. Our analysis focuses on alcids, but densities of non-alcid bird species are summarized to illustrate the importance of alcids in this ecosystem. Counts of birds were made from a vessel moving at a relatively constant speed (mean: 17 km h^{-1}, range: 13–23 km h^{-1}, depending on the vessel used and direction of wind and tidal flow). Most analyses focused on comparisons within each survey when vessel speeds were fairly constant. Most surveys were made from the M.V. *Alta* and M.V. *Sea Otter* (both with eye-level 2.0–3.0 m above the sea), but one survey, on 5 June 1995, was done from a large, rigid-hull, inflatable boat (eye-level 1.5 m above the sea). With our narrow transect strip, variable boat size was not considered to produce a bias. Two observers were on duty at all times; each scanned an area ahead of the vessel and out to 150 m on either side of the vessel. Observers were trained to estimate distances with reference to known distances. Birds on the water and flying within the transect boundaries were counted separately. Analysis focused on densities of alcids seen on the water within the transect strip, which were considered more likely to reflect foraging distributions than flying birds.

Surveys were usually restricted to periods when wind and seas were at Beaufort sea state 3 or less (winds <5.5 m s^{-1} and breaking wavelets rare), but data were collected during a few brief periods

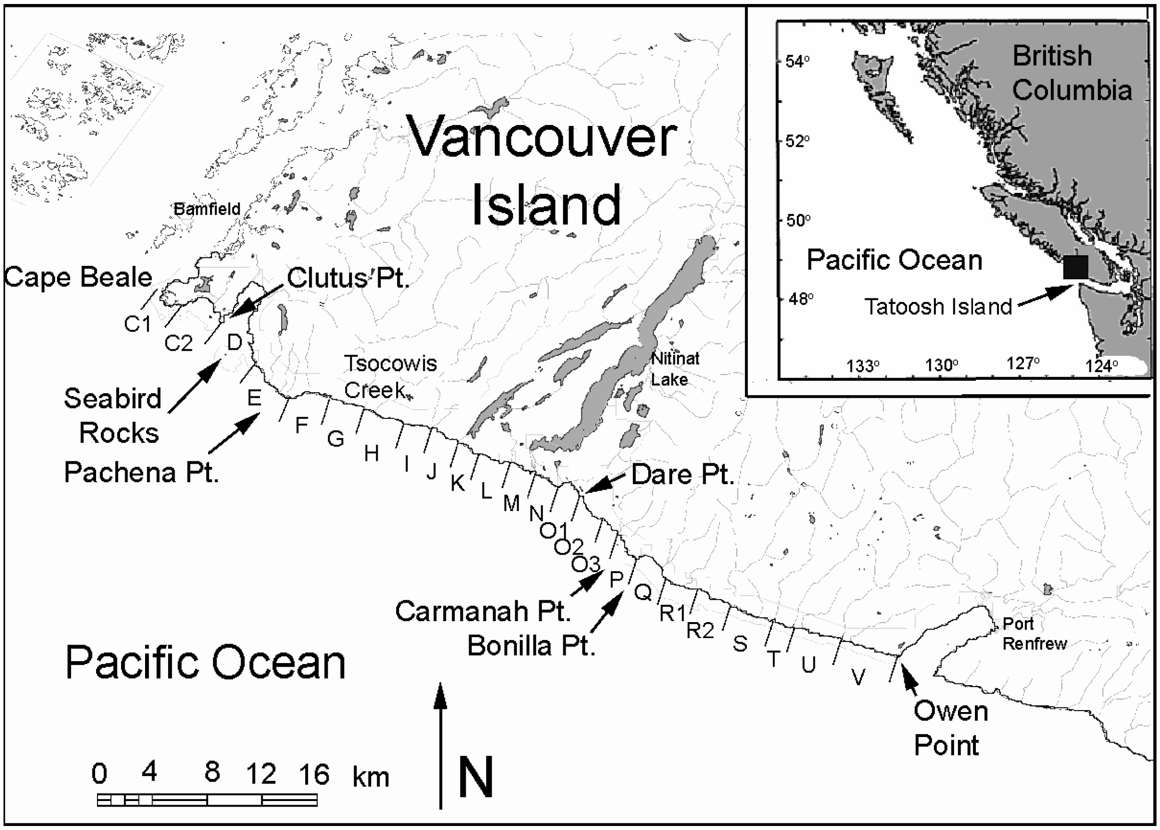

Fig. 1. Map of the study area off southwest Vancouver Island, showing the 24 sectors (C1 through V) sampled in longshore transects between Cape Beale and Owen Point.

of stronger winds to ensure continuity of the transects. Navigation was with reference to known landmarks along the coast (GPS was not always available), and the transect was divided into 24 sectors of unequal length bounded by conspicuous landmarks, which have traditionally been used in the park for inventory and management (Fig. 1). Sector length averaged 2.8 ± 0.9 (SD) km (range: 1.5–4.5 km).

In addition to the transects parallel to the shore, we also sampled alcid distributions on 27 June 1994 along 11 transects (300 m wide; 2–3 km in length) perpendicular to the shoreline at randomly chosen points between sectors C2 and O2 (Fig. 1). Alcid numbers and sea depth (measured with a sounder) were measured in 250-m intervals in each transect. The vessel was generally able to approach no closer than 50 m to the shore because of waves and shallows, but no birds were seen between the closest point and the shore.

Data analysis.—We used a two-factor analysis of variance (ANOVA; SAS, version 9.1; SAS Institute, Cary, North Carolina) to test the effects of month, zone, and a month*zone interaction on the densities (log-transformed) of each species. Spatial distribution of birds on the longshore transects was assessed at two scales. First, for all data from 1993–1996, we compared the densities of birds within each of the 24 sectors along the coast, treating the inner and outer zones separately. The mean coefficient of variation (CV; Zar 1996) across the 24 sectors was calculated to indicate the variability of density and sector use for each species. Second, finer-scale analysis was possible using data collected in 1995–1996 in 1-min intervals (~280 m of travel). These fine-scale data were used to calculate spatial aggregations of each species using the univariate neighbor-K method (O'Driscoll 1998, Davoren 2000, O'Driscoll et al. 2000, Davoren et al. 2002) and following the same approach as Burger et al. (2004). The univariate method compares the number of conspecifics occurring within patches of increasing radius with the numbers expected from random distributions of the species along the transect length. In the neighbor-K analysis of each survey, we calculated patch radius (also known as "patch length" or "ambit"), defined as the radius at the first peak in the difference between expected neighboring birds and the random distribution. Patch radius gives the spatial scale (km) at which aggregations occur (O'Driscoll 1998, Burger et al. 2004). Univariate neighbor-K analyses were applied to surveys that had more than five individual birds per species or group being analyzed.

The bivariate neighbor-K method (O'Driscoll 1998) tests for aggregation (clumping) or segregation (avoidance) of one species in relation to another (Davoren 2000, O'Driscoll et al. 2000, Davoren et al. 2002, Burger et al. 2004). Significant aggregations can be detected by the presence of peaks in the plot of neighbor-K statistics, indicating the spatial scale at which the distribution of a bird species or group was significantly clumped or overdispersed in relation to the distribution of the other group. Conversely,

TABLE 1. Mean densities (± SE) of birds (birds km^{-2}) recorded on the water or flying in longshore surveys along the West Coast Trail, Vancouver Island, in June–August, 1993–1996. Means and SE were calculated from the overall densities per survey over the entire transect length.

	Birds on water		Birds flying	
Species or group	Inner zone[a]	Outer zone[b]	Inner zone[a]	Outer zone[b]
Alcids				
Marbled Murrelet	45.16 ± 10.08	10.57 ± 3.95	2.41 ± 0.57	1.22 ± 0.46
Common Murre	11.16 ± 4.16	16.57 ± 3.78	0.93 ± 0.40	1.23 ± 0.42
Rhinoceros Auklet	5.78 ± 1.35	5.80 ± 1.12	0.54 ± 0.10	0.44 ± 0.07
Tufted Puffin (*Fratercula cirrhata*)	0.02 ± 0.01	0.02 ± 0.02	0.00	0.00
Pigeon Guillemot	0.78 ± 0.16	0.49 ± 0.15	0.33 ± 0.12	0.20 ± 0.06
Cassin's Auklet (*Ptychoramphus aleuticus*)	0.11 ± 0.06	0.28 ± 0.14	0.00	0.06 ± 0.04
Other species				
Loons (*Gavia* spp.)	0.89 ± 0.29	0.13 ± 0.10	1.13 ± 0.44	0.14 ± 0.06
Grebes (*Podiceps* spp.)	0.07 ± 0.05	0.05 ± 0.05	0.00	0.01 ± 0.01
Sooty Shearwater (*Puffinus griseus*)	0.01 ± 0.01	0.12 ± 0.10	0.03 ± 0.03	0.11 ± 0.11
Cormorants (*Phalacrocorax* spp.)	2.16 ± 0.31	2.14 ± 1.52	2.29 ± 0.31	0.73 ± 0.18
Scoters (*Melanitta* spp.)	14.93 ± 3.83	0.98 ± 0.69	1.37 ± 0.44	0.62 ± 0.35
California Gull (*Larus californianus*)	7.24 ± 2.19	30.10 ± 10.66	7.02 ± 2.82	8.27 ± 3.23
Glaucous-winged Gull (*L. glaucescens*)	0.60 ± 0.21	0.42 ± 0.31	0.95 ± 0.50	1.89 ± 1.65
Other gull species (*Larus* spp.)	1.02 ± 0.56	1.22 ± 0.61	0.82 ± 0.77	0.28 ± 0.19
Phalaropes (*Phalaropus* spp.)	0.54 ± 0.33	0.38 ± 0.30	0.21 ± 0.14	1.24 ± 0.99
Total all species	90.49 ± 11.12	69.26 ± 11.68	18.04 ± 3.12	16.43 ± 2.81

[a] $n = 13$ surveys; mean distance: 65.4 ± 1.2 (SE) km.

[b] $n = 10$ surveys; mean distance: 65.8 ± 0.8 (SE) km.

segregation between species is indicated by a trough, where fewer of the comparison species occur within a patch than expected from a random distribution.

RESULTS

Density of birds, distance from shore, and seasonal trends.—Alcids were numerically dominant in both the inner and outer zones, making up 62% and 43%, respectively, of the combined densities of all birds on the water and flying (Table 1). Murrelets made up 44% of the birds in the inner zone, but only 14% in the outer zone. By contrast, murres and auklets had similar densities in the inner and outer zones. Densities of guillemots were slightly higher in the inner zone.

Eleven transects perpendicular to the shoreline on 27 June 1994 showed the distribution of alcids 50–2,800 m from shore (Fig. 2). When binned in 250-m intervals in relation to the shoreline, the distributions of murres and auklets showed no significant differences ($\chi^2 = 7.615$, df = 4, $P > 0.05$), but distributions of murrelets differed significantly from the pooled counts of murres and auklets ($\chi^2 = 52.03$, df = 4, $P < 0.001$). Guillemots were not seen in these transects. Murrelets were strongly associated with shallow water near shore: 77% of all the murrelets on the water were within 550 m of shore (usually <20 m deep), and all were within 2 km of shore (usually <40 m deep).

Densities of murrelets declined from June through August, whereas densities of murres, guillemots, and auklets increased in the same period (Fig. 3). For murrelets, both month and zone had significant effects on density (two-factor ANOVA, $F = 44.31$, df = 2, and $F = 44.95$, df = 1, respectively; $P < 0.001$ in each case). Murre densities were not significantly affected by month or zone ($P > 0.05$), though there was a substantial increase in August. Month had a significant effect on both auklets ($F = 16.91$, df = 1, $P < 0.001$) and guillemots ($F = 4.04$, df = 2, $P = 0.037$), but zone did not ($P > 0.1$). The month*zone interaction was not significant for any of the alcid species ($P > 0.05$), which suggests that the monthly trends were similar in both zones and there were no marked shifts in spatial distribution in relation to the shoreline during this period.

Longshore spatial distribution of birds: Coarse scale.—Bird densities in each of the 24 sectors along the coast were calculated separately for the inner and outer transects (Fig. 4). Densities of murrelets were consistently higher in the inner zone between Tsocowis Creek and Bonilla Point (sectors H–Q). Murrelet densities per sector in the outer zone were lower and less consistent among the years than in the inner zone. High densities of murres occurred in the northern end (sectors C1–D) and in sectors O1–O3. Auklets were usually concentrated near their colony at Seabird Rocks (sectors C1–D) but showed little consistency in their use of the remaining sectors. Guillemots, the least common of the four alcid species, showed variable use of the sectors; consistently high densities were recorded near Seabird Rocks, where many guillemots breed (sectors C2–E), and in several other sectors scattered along the coastline where small numbers nested. As indicated by the CV, murrelets in the inner zone had the most consistent densities within each longshore sector, murres and auklets were intermediate, and guillemots showed the most variation in sector use (Fig. 4).

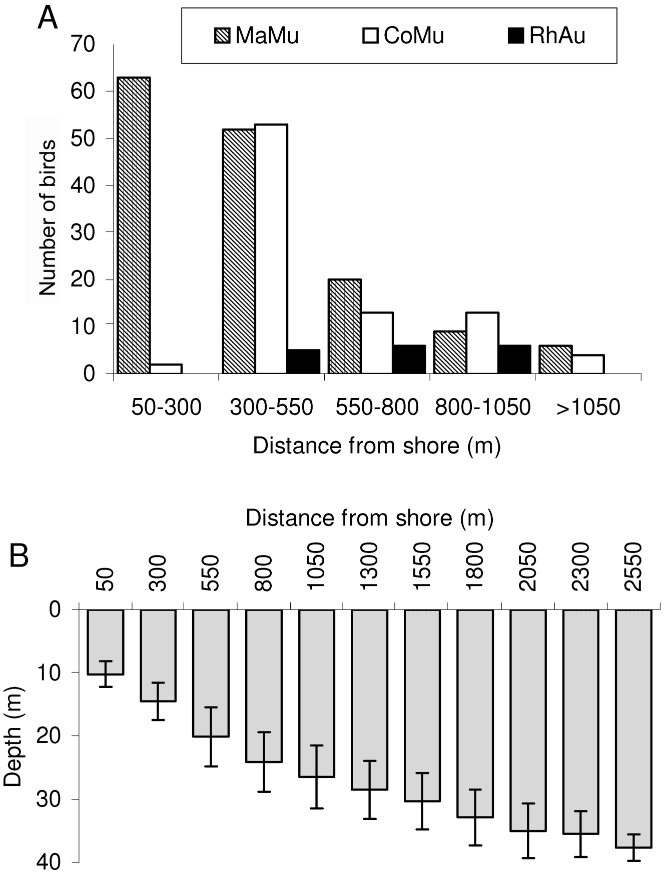

Fig. 2. (A) Sum of the counts of Marbled Murrelets (MaMu), Common Murres (CoMu), and Rhinoceros Auklets (RhAu) and (B) mean (± SD) sea depth plotted against perpendicular distance to the shore along the West Coast Trail. Data were from 11 perpendicular transects on 27 June 1994; only birds on the water within the 300-m transect strip were included.

Mean densities of the four alcids within each sector were compared using Spearman rank correlations (Table 2). In the inner zone, only murres and auklets showed significant positive correlations in their use of the 24 sectors. In the outer zone, there was greater similarity among species in their use of sectors, and all comparisons, except those of guillemots with murrelets or auklets, showed significant positive correlations. This suggests some spatial separation among species in the waters <350 m from shore, where most murrelets and guillemots foraged, but less spatial separation in the waters 450–750 m offshore.

Longshore spatial distribution of birds: Fine scale.—Counts of birds in 1-min intervals (~280 m travel) were made in 1995–1996. The univariate neighbor-K analysis indicated significant spatial aggregations for all four alcid species in most transects. In the inner zone, significant aggregations were found in 86% of surveys for murres ($n = 7$ surveys with sufficient data), 83% for guillemots ($n = 6$), and 100% for both murrelets ($n = 8$) and auklets ($n = 7$). All outer-zone surveys with sufficient numbers for testing showed aggregations for murrelets ($n = 6$), murres ($n = 6$), auklets ($n = 6$), and guillemots ($n = 3$). Significant spatial aggregations of murrelets occurred across larger areas (radius 8–10 km) than

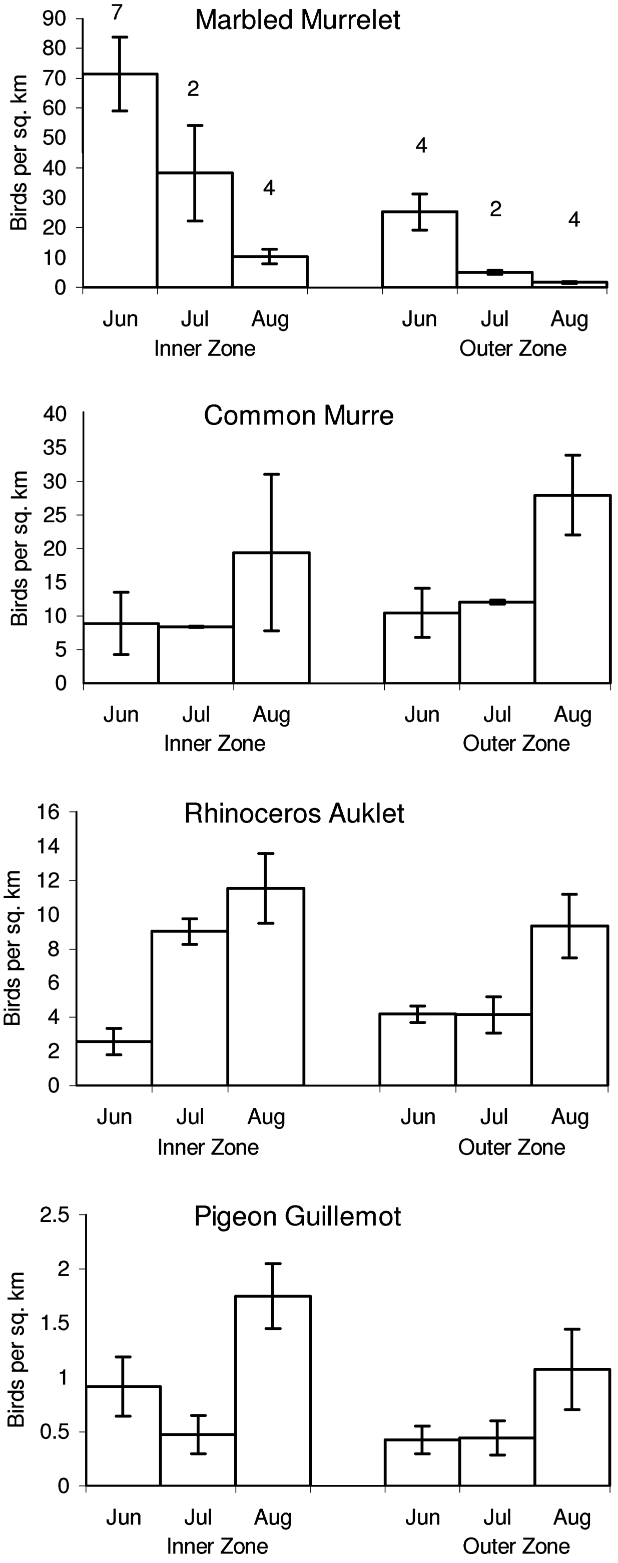

Fig. 3. Monthly mean (± SE) densities of alcids along the West Coast Trail in summer, 1993–1996. Sample sizes are the number of surveys per month. Note that the scale varies on the *y* axes.

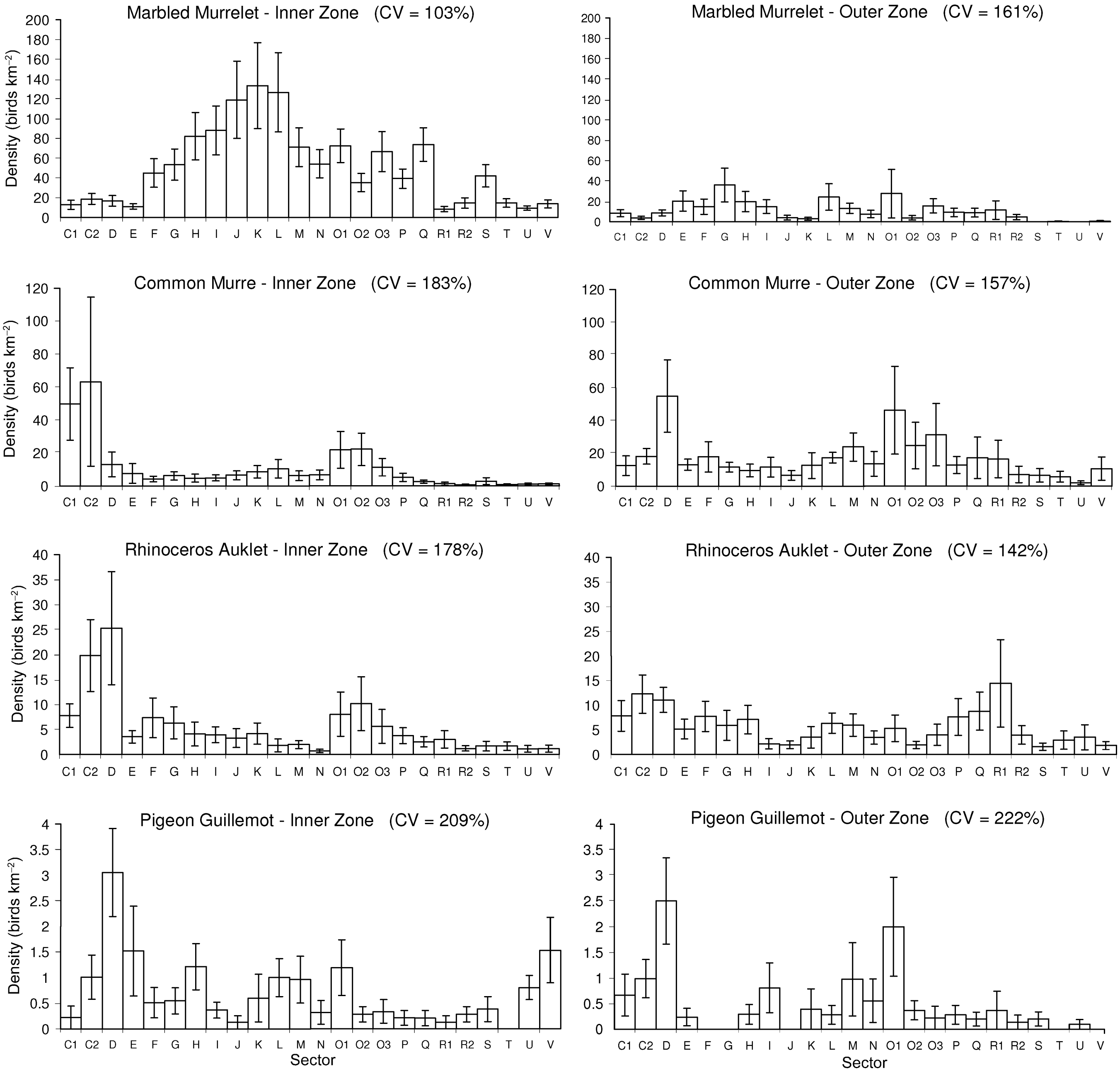

FIG. 4. Mean densities (± SE) of the four alcid species within the inner and outer zones, broken down by transect sector (see Fig. 1). Data were from 13 transects in the inner zone and 10 in the outer zone. Only birds seen on the water were included. The mean coefficient of variation (CV) is shown to indicate the consistency of use of the 24 sectors by each species. Note that the scale on the *y* axes varies among species.

those of other alcids (i.e., murrelets were spread out and not in tight flocks; Table 3).

Bivariate neighbor-K analyses were used to test for positive associations (aggregation) or negative associations (segregation) among the four alcids (Table 4). Some species pairs showed both aggregation and segregation (at differing spatial scales) within the same survey, but in those cases, the interaction that occurred with the smallest patch radius was considered the primary interaction. Some surveys showed no significant interactions among species pairs. The bivariate results were not symmetrical; for example, within the inner zone, murrelets (Bird 2) showed negative responses to the presence of murres (Bird 1; Table 4, row 1), but murres showed both negative (four surveys) and positive (three surveys) associations with murrelets (Table 4, row 5). Murrelets also showed negative responses to auklets and guillemots more often than positive responses in the

Table 2. Spearman rank correlation coefficients from comparisons of mean densities of the fish-eating alcids per transect sector along the West Coast Trail in 1993–1996. The upper right set of correlation coefficients refers to the inner-zone transect and the lower left set to the outer zone ($n = 24$ sectors for all comparisons).

	Marbled Murrelet	Common Murre	Rhinoceros Auklet	Pigeon Guillemot
Marbled Murrelet	—	0.253 ($P = 0.233$)	0.017 ($P = 0.936$)	0.075 ($P = 0.728$)
Common Murre	0.582 ($P = 0.003$)	—	0.584 ($P = 0.003$)	0.072 ($P = 0.737$)
Rhinoceros Auklet	0.452 ($P = 0.027$)	0.423 ($P = 0.039$)	—	0.159 ($P = 0.457$)
Pigeon Guillemot	0.207 ($P = 0.331$)	0.489 ($P = 0.015$)	0.331 ($P = 0.114$)	—

Table 3. Mean (± SE) patch radius (km) for aggregations of alcid species, and for birds of all species, as indicated by neighbor-K analysis. Only birds seen on the water were included here. Sample sizes are surveys in which significant univariate neighbor-K aggregations were found.

Species	Inner zone	Outer zone	Overall
Marbled Murrelet	8.82 ± 3.04 ($n = 8$)	9.66 ± 3.83 ($n = 6$)	9.18 ± 2.30 ($n = 14$)
Common Murre	1.35 ± 0.33 ($n = 6$)	4.01 ± 1.32 ($n = 6$)	2.68 ± 0.76 ($n = 12$)
Rhinoceros Auklet	4.32 ± 2.45 ($n = 7$)	2.01 ± 0.64 ($n = 6$)	3.25 ± 1.34 ($n = 13$)
Pigeon Guillemot	1.62 ± 0.68 ($n = 5$)	1.12 ± 0.56 ($n = 3$)	1.44 ± 0.46 ($n = 8$)
All alcids	9.42 ± 3.47 ($n = 8$)	7.24 ± 2.89 ($n = 7$)	8.40 ± 2.23 ($n = 15$)
Birds of all species	11.94 ± 4.02 ($n = 8$)	8.28 ± 3.40 ($n = 7$)	10.23 ± 2.62 ($n = 15$)

inner zone, but not in the outer zone. Murres and auklets were positively associated in most surveys. Guillemots did not show consistent associations with either murres or auklets. Segregation was found more often in the inner zone than in the outer zone. The spatial scale (radius) of these interactions varied considerably. Aggregation usually occurred at smaller spatial scales than segregation, except when murrelets were compared with murres or auklets.

We also calculated neighbor-K statistics comparing murrelets with the pooled counts of their most likely competitors (murres and auklets). Murrelets showed segregation with the combined murre–auklet group in five out of seven surveys in the inner zone but showed both aggregation (three surveys) and segregation (two) in the outer zone (Table 4). The combined murre–auklet group showed both aggregation (four surveys) and segregation (three) in relation to murrelets in the inner zone, and aggregation in four of the six surveys in the outer zone.

We were interested in the co-occurrence of murrelets with their most likely competitors (murres and auklets) within the smallest units possible with our fine-scaled 1995–1996 data (1-min intervals, or ~280 m of transect), regardless of the spatial scale at which the neighbor-K test might show aggregation or segregation. The intention was to show how frequently these birds were close enough to interact either positively (flocking) or negatively (interference competition). Accordingly, we compared the number of murrelets found in each transect interval with the combined number of murres and auklets in that interval and plotted the proportion of murrelets co-occurring with increasing numbers of murres and auklets (Fig. 5). On average, in the inner zone, 68% of murrelets were in intervals with no murres or auklets, and 96% were in intervals with ≤5 of these birds; in the outer zone, these values were 42% and 80%, respectively. This pattern was attributable to three factors: (1) avoidance by murrelets of murres and auklets occurring at larger spatial scales (as indicated by the neighbor-K analysis); (2) the high frequency of transect intervals with few or no murres and auklets, which, in turn, was a function of the variable densities and clumped distributions of these two species; and (3) differences in the seasonal patterns of abundance between murrelets and the murre–auklet group (Fig. 3), which affected factor 2. Therefore, at the smallest spatial scales at which positive (flocking) or negative (avoidance or competition) interactions might be expected, murrelets seldom encountered large numbers of other alcids.

DISCUSSION

Importance of the West Coast Trail waters for alcids.—In June–August, densities of all four alcid species were higher in the nearshore waters of our study area than in the adjacent shelf waters farther offshore (Burger et al. 2004). Our data confirm that the West Coast Trail waters support one of the highest densities of Marbled Murrelets in the species' range (Burger 1995, 2002; Piatt et al. 2006). By showing consistent patterns of spatial distributions, our data help management and contingency planning for the threatened murrelet and other alcids within Pacific Rim National Park Reserve.

Niche overlap among the piscivorous alcids.—Our goal was to compare the distributions of murrelets and the other common piscivorous alcids as a first step in identifying important habitat parameters and possible competitive interactions. More detailed research on prey distribution and oceanic variables is underway to help explain the observed site preferences of the murrelet (R. Ronconi unpubl. data). Understanding of regional marine habitat use and interspecific interactions is needed for conservation of this species; its marine life has received far less attention than its nesting-habitat use and inland activities (Ralph et al. 1995, Burger 2002, McShane et al. 2004, Piatt et al. 2006). Comparison with other fish-eating alcids could reveal factors important to all

Table 4. Results of bivariate neighbor-K analysis comparing the spatial aggregation (positive association) or segregation (negative association) among the four fish-eating alcid species: Marbled Murrelet (MaMu), Common Murre (CoMu), Rhinoceros Auklet (RhAu), and Pigeon Guillemot (PiGu). Only birds counted on the water were considered. The bivariate analysis considers the association of Bird 2 individuals within the radius of Bird 1 individuals (e.g., the first row considers how Marbled Murrelets respond to the presence of Common Murres). Mean (± SE) radius of significant aggregation or segregation is given.

			Aggregation most evident		Segregation most evident		Neither interaction
Bird 1	Bird 2	Sample surveys	Surveys	Radius (km)	Surveys	Radius (km)	Surveys
Inner zone							
CoMu	MaMu	7	0	—	5	11.09 ± 4.90	2
RhAu	MaMu	7	2	8.12 ± 5.60	3	11.57 ± 2.56	2
CoMu+RhAu	MaMu	7	1	1.68	5	9.74 ± 2.63	1
PiGu	MaMu	6	1	14.84	3	15.40 ± 6.08	2
MaMu	CoMu	7	3	7.09 ± 3.30	4	5.11 ± 2.72	0
RhAu	CoMu	7	7	2.44 ± 0.69	0	—	0
PiGu	CoMu	6	0	—	3	18.57 ± 1.73	3
MaMu	RhAu	7	3	6.16 ± 3.78	4	3.78 ± 1.64	0
CoMu	RhAu	7	6	2.66 ± 0.86	0	—	1
PiGu	RhAu	6	1	8.68	2	19.32 ± 5.32	3
MaMu	CoMu+RhAu	7	4	11.76 ± 7.21	3	7.19 ± 1.08	0
MaMu	PiGu	6	3	4.39 ± 1.66	3	7.19 ± 1.57	0
CoMu	PiGu	6	2	2.10 ± 0.98	2	19.46 ± 0.98	2
RhAu	PiGu	6	2	15.12 ± 11.76	3	10.17 ± 4.69	1
Outer zone							
CoMu	MaMu	6	4	7.56 ± 3.15	2	1.82 ± 0.42	0
RhAu	MaMu	6	6	3.50 ± 2.18	0	—	0
CoMu+RhAu	MaMu	6	3	8.31 ± 3.68	2	2.66 ± 1.26	1
PiGu	MaMu	3	1	4.48	0	—	2
MaMu	CoMu	6	5	8.57 ± 3.24	0	—	1
RhAu	CoMu	6	5	6.05 ± 2.85	1	5.32	0
PiGu	CoMu	3	2	3.22 ± 2.38	0	—	1
CoMu	RhAu	6	6	5.74 ± 2.55	0	—	0
MaMu	RhAu	6	4	5.25 ± 2.97	2	3.36 ± 0.00	0
PiGu	RhAu	3	2	15.26 ± 10.50	0	—	1
MaMu	CoMu+RhAu	6	4	6.93 ± 3.14	1	3.92	1
MaMu	PiGu	3	2	6.72 ± 2.24	1	2.24	0
CoMu	PiGu	3	3	2.71 ± 1.47	0	—	0
RhAu	PiGu	3	3	6.53 ± 4.37	0	—	0

members of the guild, and also interspecific interactions that may affect the murrelets.

The species and size classes of prey taken by murrelets, murres, and auklets off Vancouver Island overlap considerably, as shown by analyses of prey (Carter 1984, Vermeer et al. 1987, Hay et al. 1992, Burkett 1995, Gaston and Jones 1998, Davoren and Burger 1999, Davoren 2000) and stable isotopes (Hobson 1990, Hobson et al. 1994). The diets of these birds are dominated by Sand Lance (*Ammodytes hexapterus*) of all age classes, juvenile Herring (*Clupea harengus*), and, to a lesser extent, Northern Anchovy (*Engraulis mordax*), smelt (*Allosmerus elongatus* and *Hypomesus pretiosus*), juvenile salmonids (*Oncorhynchus* spp.), immature rockfish (*Sebastes* spp.), and other small schooling fish. Similarities in diet among these alcid species have been reported elsewhere (Sanger 1987, Vermeer et al. 1987, Burkett 1995, Lance and Thompson 2005). There is, therefore, scope for interspecific competition for such prey where large numbers of these three species co-occur.

Guillemots, by contrast, take primarily solitary, benthic fish species and, occasionally, epipelagic schooling species (Vermeer et al. 1987, Ewins 1993). In addition, our data indicate differences in nearshore habitat use between guillemots and other alcids. Guillemots were concentrated near Seabird Rocks (sectors C2–E), where many of them nest, and in smaller numbers at scattered sites along the entire coastline. Guillemots were the only species to show high use of the southern extremity of the study area (sectors R1–V), which had a rocky, often cliff-faced shoreline offering nest sites. Overall, there seems to be little niche overlap between guillemots and other alcids, and our discussion, therefore, focuses on murrelets, murres, and auklets.

Niche separation by diving abilities was unlikely in our study area, where waters <40 m deep were within the diving abilities of all the piscivorous alcids (Burger 1991, Mathews and Burger 1998) and most prey were in the upper 10 m (Burger et al. 2004, A. E. Burger unpubl. data).

Spatial distributions of murrelets, murres, and auklets.— Although there was considerable overlap (Figs. 2 and 4), our data show significant differences in spatial distribution between murrelets and the other fish-eating alcids, whereas the distributions of murres and auklets were very similar. Murrelets were strongly

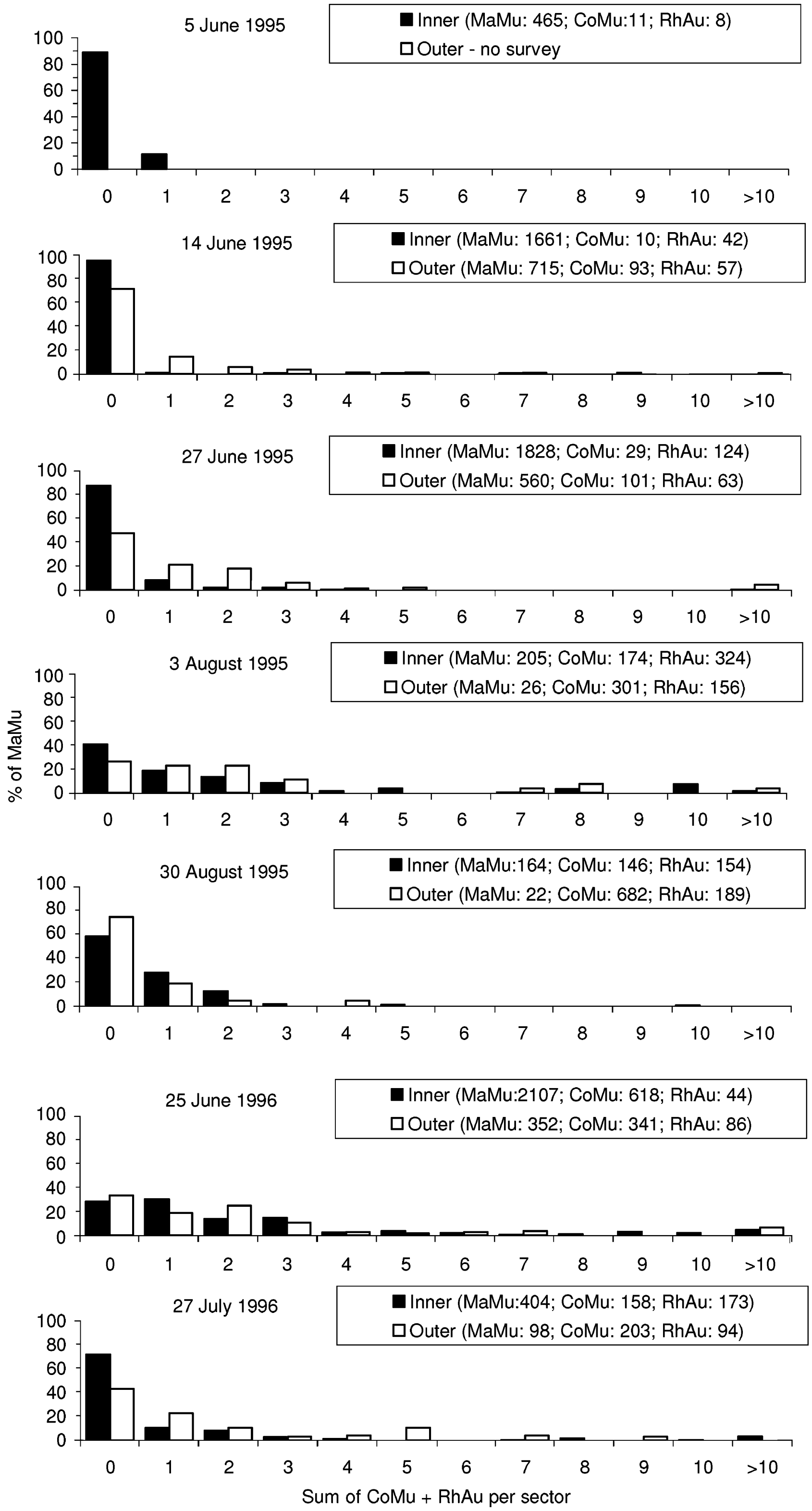

FIG. 5. Percentage of the total count of Marbled Murrelets (MaMu) within each transect that co-occurred with Common Murres (CoMu) and Rhinoceros Auklets (RhAu) in 1-min (~280 m) sectors of the transect. Murrelets were usually found in sectors that contained few Common Murres or Rhinoceros Auklets. Only birds on the water within the transect strip were considered. Numbers of each species are shown in the legends.

associated with waters within 600 m of shore (see also Burger 1995), but murres and auklets were more evenly distributed across the coastal waters that we sampled. Murres, and to a lesser extent auklets, were also common farther offshore over the continental shelf, where murrelets were rare (Morgan et al. 1991, Burger et al. 2004).

We also found differences in the longshore distribution of the four alcids. Consistent year-to-year use of preferred sectors, especially those in the inner zone, was less evident for murres, auklets, and guillemots than it was for murrelets. Within the inner zone, densities per transect sector were significantly correlated between murres and auklets but not for any other species. In the outer zone, there were significant correlations involving all four species. The bivariate neighbor-K analysis indicated negative spatial clustering (segregation) between murrelets and murres, especially in the inner zone, and, to a lesser extent, between murrelets and auklets. By contrast, murres and auklets were usually positively associated (aggregated) in both inner and outer zones.

The univariate neighbor-K analysis showed that spatial aggregation by murrelets occurred over larger areas (mean radii: 8–9 km) than for murres and auklets (1–4 km). This reflects the tendency of murrelets to forage singly or in pairs, with loose aggregations spread over large areas (Nelson 1997), whereas murres and auklets are more likely to forage in larger, tighter flocks (Gaston and Jones 1998). The spatial aggregations of murres and auklets are typical of seabirds foraging in shelf or upwelling ecosystems (typically 2–8 km; Burger et al. 2004, Ainley et al. 2005, and studies cited therein). Evidently, the foraging aggregations of murrelets were determined by somewhat different social and biological factors than those of murres and auklets. The bivariate neighbor-K analyses suggest that both aggregation and segregation among species were most evident at spatial scales of several kilometers, which is likely a function of spatial clustering (as indicated by the univariate results), similarities or differences in habitat use among species, and possible avoidance behavior (see below). Both univariate and bivariate neighbor-K results indicate the spatial scales at which such factors should be investigated.

Some of the differences in spatial distribution along the coast can be attributed to the location of breeding sites. Auklets nest on Seabird Rocks, which partly explains their high densities in that area (sectors C2 and D). Murres do not breed within the study area, but there is a colony of ~2,000 pairs nearby on Tatoosh Island, off the tip of the Olympic Peninsula (Parrish et al. 2001), 25 km south of Carmanah Point. We saw murres carrying fish toward this colony from our study area, and dozens of adults accompanied by recently fledged chicks were found here each summer. The densities of murres, however, were lowest in sectors R1 through V, close to Tatoosh Island, and were often highest in sectors farthest from the colony (C1 and C2). Likewise, proximity to forested nesting habitat does not fully explain the marine distribution of murrelets in our study area. Although concentrations of murrelets generally occurred adjacent to watersheds with some likely nesting habitat, the largest area of suitable forest was within Carmanah–Walbran Provincial Park, adjacent to sectors Q–S, which did not contain the highest concentrations of murrelets. Murrelets are known to commute tens of kilometers from foraging grounds to nest sites (Whitworth et al. 2000, Hull et al. 2001), and our entire study area would, therefore, be within a comfortable commuting distance of adjacent inland forests. Overall, as reported in some other studies (Ainley and Boekelheide 1990, Haney and Schauer 1994), proximity to breeding sites did not consistently affect seabird densities and spatial distribution at the spatial scale of our investigation.

Evidence of possible interspecific competition.—We found strong similarities between the distributions of murres and auklets at a range of spatial scales, whereas the distribution of murrelets differed with those of both species, especially in the inner zone. At the smallest scale (~280 m), murrelets seldom encountered murres or auklets. These patterns may be attributable to subtle differences in foraging strategies and habitat preferences among the species, but we cannot rule out the possibility that murrelets were affected by interspecific competition.

Competition among foraging seabirds could be mediated through three processes: exploitative competition (resource depletion, e.g., Birt et al. 1987), active interference competition (aggression or the perception of aggression; Piatt 1987, 1990), and passive interference competition (e.g., disruption of prey schools to make them less available; Lewis et al. 2001, Ainley et al. 2003). Species-specific habitat use among these alcids is unlikely to be driven by resource depletion. Murres, auklets, and other seabirds continued to move into our study area from June through August, and year-round hydroacoustic surveys in the adjacent shelf waters showed highest prey abundance in July through September (Burger et al. 2004).

Interference competition is possible, however, whereby murrelets avoid areas frequented by murres and auklets, either because they are afraid of these larger alcids (active) or because the murres and auklets somehow make prey less available to murrelets (passive). We are unable to differentiate the mechanism but believe that the spatial and temporal trends in distribution that we documented indicate the possibility of such competition. Piatt (1990) invoked interference competition to explain the spatial segregation between two alcid species, Common Murres and Atlantic Puffins, off Newfoundland, and he reported aggressive behavior by murres directed at the smaller Atlantic Puffins (Piatt 1987). Interspecific interference competition also occurs within mixed-species feeding flocks in the northeast Pacific (Hoffman et al. 1981, Ainley and Boekelheide 1990, Maniscalco et al. 2001). We have not seen aggressive interactions among the species, but aggressive interactions need not be common for higher vertebrates to avoid such encounters if there is a perception of risk (Brown et al. 1999, Preisser et al. 2005). Murrelets are known to avoid the large, multispecies foraging flocks that are a common feature of this area in summer, whereas murres and auklets frequently participate (Porter and Sealy 1981, 1982; Chilton and Sealy 1987). Elsewhere in British Columbia, on fjords, straits, and inlets where larger alcids are rare, murrelets regularly form mixed feeding flocks with gulls (Mahon et al. 1992), which indicates that it may be the presence of other pursuit-diving seabirds (larger alcids and, perhaps, cormorants and shearwaters) that deter them from joining large mixed flocks on the outer coast (Chilton and Sealy 1987).

Avoidance of areas frequented by larger alcids may also explain the puzzling seasonal changes in density of murrelets in our study. Murrelets began to leave our study area as their breeding ended after mid-July, and most were gone by mid-August. This exodus occurred at the same time that densities of murres and auklets were increasing because of a postbreeding influx of birds (Fig. 3). Near-surface schools of small, immature Sand Lance and Herring remain common in the area through August (Hourston 1958, Hay et al. 1992, Davoren 2000; and informal observations made during the present study). The exodus of murrelets is, therefore, not simply explained by reduced prey abundance, though there may be some subtle changes in prey availability that are not obvious to us.

Implications for management and monitoring.—Whether caused by interspecific competition or by other niche-selective forces, differences in spatial distribution of murrelets compared with other piscivorous alcids need to be taken into account in the management and monitoring of this threatened species. Because of the difficulties of finding and observing murrelets at nest sites, it is nearly impossible to monitor their breeding success, diets, chick growth, and other indicators of population health. Analysis of isotopes provides valuable retrospective trends in trophic niches (Becker and Beissinger 2006, Becker et al. 2007, Norris et al. 2007), but murrelets have to be caught at sea to provide such samples, which precludes affordable ongoing monitoring. Diets, chick growth, breeding success, and adult condition can be readily monitored with colonial-nesting seabirds, such as murres and auklets. It is tempting to extrapolate from data collected on colonial species to imply causal effects on murrelets, including likely effects of oceanic variations and global climate change (McShane et al. 2004). The differences in habitat use and timing of movements by murrelets in our study area, compared with murres and auklets, suggest caution in extrapolating trends seen in these colonial alcid species to murrelets.

Murrelets overlap with larger species of piscivorous alcids throughout most of their range. Interactions with these species might affect the distribution, foraging behavior, seasonal movements, and even population trends of murrelets and, therefore, need to be considered in conservation and monitoring plans for murrelets. More information is needed on similarities and differences in prey, foraging behavior, fine-scale habitat use, and interspecific interactions, to confirm the role that other species play in the marine activities of the piscivorous alcid guild.

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