USING RADAR TO ESTIMATE POPULATIONS AND ASSESS HABITAT ASSOCIATIONS OF MARBLED MURRELETS

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***Abstract*:** I used high-frequency marine radar to count marbled murrelets (*Brachyramphus marmoratus*) entering 20 watersheds in Clayoquot Sound, Vancouver Island, British Columbia, Canada, in 1996–1998. My goal was to develop standard protocols for radar inventory and to explain landscape-level habitat associations of this threatened species. Dawn counts were consistently higher and less variable than dusk counts, but both sampling periods produced similar rankings of watersheds and proportionate numbers of murrelets. Most dawn surveys showed a unimodal pre-sunrise pulse of incoming murrelets, but a few dawn surveys showed post-sunrise pulses, likely caused by repeat visits by some birds. These post-sunrise pulses, although rare, inflated estimates of incoming murrelets and were avoided by restricting analyses to pre-sunrise counts. Dawn and dusk counts were higher on cloudy days (≥80% cloud cover) than on clear days, but among cloudy days there was no additional effect on counts caused by precipitation (thick fog or drizzle). Numbers of murrelets entering watersheds varied seasonally, reflecting the breeding chronology, but counts restricted to the core period covering incubation and chick-rearing (mid-May through mid-Jul) showed no significant seasonal effects. Counts varied among years at some stations, but when all stations were considered together, no significant inter-annual variation occurred. Murrelets sometimes flew over low ridges (200–600 m), taking shortcuts into watersheds or crossing from 1 watershed into another. I therefore adjusted the boundaries of some inland catchment areas (based on topography and likely flight paths) to match correctly counts made at the watershed mouths with the appropriate inland catchment area. Radar counts at 18 watersheds were significantly correlated with total watershed area, areas of mature (>140 year old) forest, and—most strongly—with areas of mature forest below 600 m. Logging produced negative impacts. Three of the 5 watersheds with extensive logging of low-elevation forest had fewer murrelets per area than unlogged watersheds or those that were <10% logged, but these differences disappeared once remaining low-elevation mature forests were considered. With the removal of old-growth forests, murrelets evidently moved elsewhere and did not pack into the remaining old-growth patches in higher densities.

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The marbled murrelet is listed as threatened in both Canada and the United States. Loss of nesting habitat in old-growth coniferous forest is the primary reason for its decline (Ralph et al. 1995). Nests are cryptic and difficult to locate, and adults commute between interior nest sites primarily during dawn and dusk twilight. Consequently, it is impossible to assess stand and watershed populations from visual counts of nests or adults.

High-frequency radar (Cooper et al. 1991) has been found to be an effective tool for locating and counting murrelets as they cross from the ocean to the forest (Burger 1997, Cooper et al. 2001). No other method allows counts of murrelets entering large landscape units. Such counts are valuable in estimating local and regional populations, comparing watersheds for land-use management, assessing macrohabitat preferences of the murrelets, and tracking long-term changes in local populations. Radar inventory is, however, a new technique, and the variability in counts caused by flight behavior; weather; and diurnal, seasonal, and annual variations are poorly known (Cooper et al. 2001).

I address these issues using counts made at 20 watersheds over 3 breeding seasons. One goal of this article is to determine the most appropriate protocol for counting murrelets with radar. To this end, I examined diurnal, seasonal, and annual variations in murrelet counts; the effects of weather on radar counts and murrelet behavior; and the species and numbers of other birds likely to be confused with murrelets on radar. I also compared murrelet counts per watershed with landscape-level habitat characteristics of the watersheds and investigated the effects of clearcut logging on watershed populations.

STUDY AREA

I conducted my study from 1996–1998 in Clayoquot Sound, southwest Vancouver Island,

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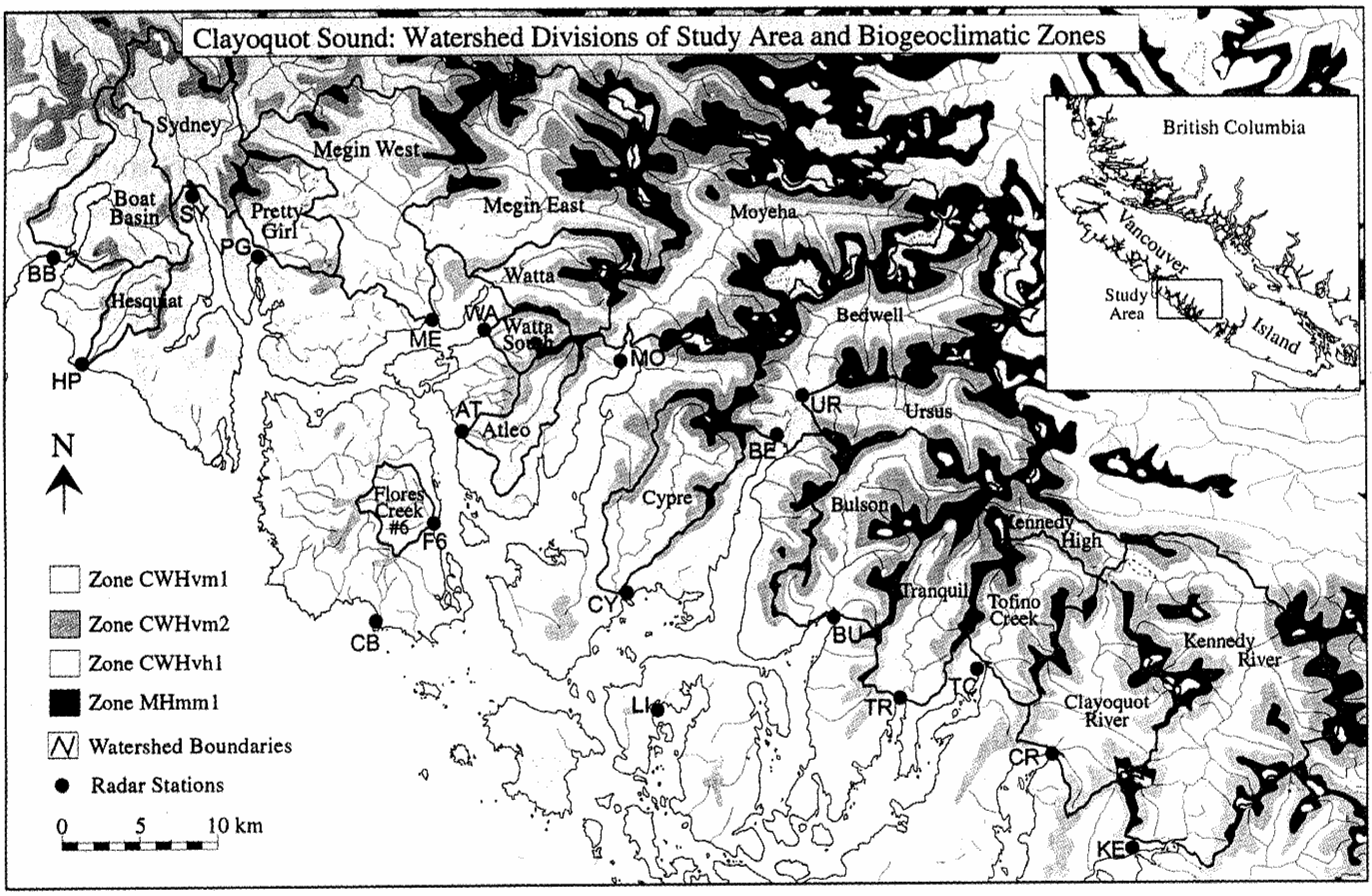

Fig. 1. Map of Clayoquot Sound showing the locations of 18 survey stations used to count marbled murrelets at the mouths of watersheds, and 1 inland station (UR) used to determine the proportions of murrelets entering the Bedwell and Ursus valleys. The Watta Station (WA) was used to simultaneously count murrelets entering the Watta and Watta South watersheds. The map also shows the areas of 18 watersheds used in habitat analysis and the distribution of the 4 biogeoclimatic zones.

British Columbia, Canada (Fig. 1). The area supports 1 of the highest concentrations of breeding marbled murrelets south of Alaska, including more than 10% of the estimated provincial population (Rodway et al. 1992, Burger 1995). Large tracts of old-growth forest suitable as nesting habitat lie adjacent to productive nearshore foraging areas (Sealy and Carter 1984, Kelson et al. 1995). Management and conservation of this murrelet population is of global importance.

Watersheds opening into narrow inlets where murrelets are funnelled through a narrow flyway can be more reliably counted with radar than those with wide coastal access (Burger 1997). Clayoquot Sound, where most watersheds drain into narrow fjords, is ideal for radar counts. Eighteen radar stations on the coast were used to sample 20 watersheds, which included the bulk of available nesting habitat around Clayoquot Sound (Fig. 1, Appendix 1). At Watta Station (WA) the birds entering 2 watersheds could be simultaneously counted (Watta and Watta South). Counts made at the Bedwell River mouth (BE) included murrelets using the Bedwell and adjoining Ursus valleys. An inland station (UR) was used to separate the Bedwell mouth counts into those entering the Bedwell (25% of birds) and Ursus (75%) valleys (Burger 1999). I applied this division to habitat analyses because the Bedwell and Ursus had different logging histories (Burger 1999), but not to other analyses. Data from Lemmen's Inlet (LI) and Cow Bay (CB) stations were insufficient for habitat analysis (see below) but were included in other analyses.

METHODS

My methods followed those of Burger (1997). Observers used 2 mobile radar units: a Furuno FR-7111 and a Furuno FR-810D. Both were 10 kW marine surveillance models using 9410 MHz (X-band) transmitted through 2 m scanners. Each scanner was tilted upward and scanned a vertical arc of 25°. Each unit had a vertically adjustable aluminum screen fitted along the bottom edge of the scanner in an attempt to reduce ground clutter, such as reflections from vegetation or waves (Cooper et al. 1991). Tests showed that the screen had no noticeable effect under the sampling conditions, and so it was removed from the FR-810D unit to reduce its weight. Adding or removing the anti-clutter screen had no effect on the speed of rotation of the scanner. The 2 units were operated simultaneously for 2 days at the Bedwell Station (BE) in 1998 (mounted at slightly different heights to reduce interference) and produced comparable counts of murrelets.

The scanners were usually mounted on platforms 2.5 m above the ground and positioned to provide a clear view across the expected flight path of the murrelets, at or near the mouth of each watershed. At 2 sites exposed to choppy seas (Hesquiat Point [HP] and Megin [ME]) the radar scanner was positioned on the ground, with a low barrier of logs built around it to screen out the reflections from waves. Interference from waves was not a problem in the protected waters at the other sites.

Observers set the scanning radius at 1 km at most locations and 1.5 km at 4 stations where the murrelets' flight path was beyond 1.0 km. We turned off both rain and sea scatter suppressers and turned up the gain to near-maximum to give maximum sensitivity to the signals. At these settings we readily detected murrelets, bats, and smaller birds, such as swallows. We distinguished images of marbled murrelets from those of other birds and bats by their size (smaller birds and bats produced small images), flight path (few birds, other than murrelets, flew between the ocean and the interior, or had fairly straight paths), and speed (murrelets generally flew much faster than most birds; Hamer et al. 1995, Burger 1997, Cooper et al. 2001; further details below). The speeds of murrelets and other birds, visually identified by a second observer, were estimated by measuring the distance between successive images on the radar screen (which could be converted to actual distance with a precision of 10 m) divided by the time between images (3.0 sec for the FR-810D and 2.7 sec for the FR-7111). During radar surveys a second observer, positioned within 50 m of the scanner, recorded the presence of any species likely to be confused with murrelets on the radar. Between surveys, the field crew recorded the maximum daily count of such birds near the radar stations.

The protocol was to visit each station at least twice per season, with each visit lasting 2–3 days and involving dawn and dusk surveys on each day. Visits were 4–5 weeks apart. Heavy rain, equipment failure, and other logistical problems sometimes resulted in cancelled visits or reduced numbers of surveys per visit. I analyzed seasonal changes indirectly by calculating the count at each survey as a percentage of the maximum count for that year at that station (Jodice and Collopy 2000).

Dawn surveys started 90 min before sunrise and ended 60 min after sunrise, or 15 min after the last murrelet was recorded. Dusk surveys began 40 min before sunset and continued for 2 hr. I obtained sunrise and sunset times for Tofino from the Dominion Astrophysical Observatory (www.hia.nrc.ca/services/sunmoon/). Observers made standardized weather observations at the start and end of each radar survey and noted any changes likely to affect radar detections, such as the onset and cessation of rain squalls, which obscured bird images. I omitted from the analysis all surveys in which rain obscured the murrelet's flight path for >10 minutes during periods of peak activity. Weather during surveys was categorized as: clear (cloud cover <80%), cloudy (cloud cover 80% but no precipitation), and drizzle/fog (cloud cover 80%, with thick fog and/or drizzle). Standard audiovisual surveys show an increase in murrelet activity over forests when cloud cover exceeds 80% (Rodway et al. 1993*a*, Naslund and O'Donnell 1995), although the effects are not always consistent (Jodice and Collopy 2000).

I analyzed 2 flight categories (Burger 1997): incoming (direct flight inland from the ocean or inlet) and outgoing (direct flight towards the ocean or inlet). I ignored murrelets circling over the ocean or the forest. Observers noted the apparent size of each flock of murrelets and could usually separate single birds and flocks. The number of birds in flocks was difficult to determine, particularly if fewer than 4 successive images were obtained on the radar screen (Burger 1997). Observers were more likely to underestimate flock size (e.g., 3 birds recorded as 2), so estimates of numbers of birds were conservative. In addition, we probably failed to detect some murrelets flying close to treetops. Consequently, all counts underestimated the true numbers entering watersheds.

I used landscape habitat features for each watershed derived from overlays of 3 GIS digital databases: a 1:250,000 Biogeoclimatic Ecosystem Classification, from British Columbia Ministry of Forests (MOF); 1:250,000 Baseline Thematic Mapping, from British Columbia Ministry of Environment, Lands and Parks; and the 1:20,000 Clayoquot Sound Watershed atlas, from MOF. In Clayoquot Sound, where extensive clearcut logging occurred only since the 1940s and fires were rare, virtually all forests classified as mature (>140 years) were actually old-growth (>250 years), but the latter category was not available in the GIS databases. Immature (20–140 years old, but usually <60 years old) and recently logged (<20 years old) forests were combined in some analyses. The study area included 3 variants of the Coastal Western Hemlock (CWH) biogeoclimatic zone and 1 variant of the Mountain Hemlock (MM) zone: CWHvh1 (very wet hyper-maritime) occurred at elevations below 150 m in forests exposed to open ocean; CWHvm1 (submontane very wet maritime) occurred from 0–600 m in sheltered inlets but from 150–600 m at exposed shores; CWHvm2 (montane very wet maritime) occurred from 600–900 m; and MMmm1 (windward moist maritime mountain hemlock variant) occurred as sub-alpine forests above 900 m (Fig. 1; Green and Klinka 1994). I estimated the distance from each watershed mouth to the nearest foraging aggregation (Distfeed) along flight paths over the ocean. Foraging aggregations were mapped by Sealy and Carter (1984) and Kelson et al. (1995) from boat surveys that covered all of Clayoquot Sound.

To account for murrelets using the shortest access routes by crossing low ridges into neighboring watersheds, I adjusted the following watershed areas. I split the Megin watershed into West and East portions (Fig. 1). I assigned murrelets counted at the Megin Station (ME) to the West Megin, but those entering the Watta Valley mouth were assigned to the combined East Megin area and the Watta Valley. I removed the uppermost portion of the Kennedy watershed (Kennedy High; Fig. 1) from the Kennedy and assigned half of this area to each of the Tofino Creek (TC) and Clayoquot River (CR) samples, assuming that these 2 watersheds provided easier access to Kennedy High than via the full length of the Kennedy Valley. Undoubtedly, other movements among adjacent watersheds occurred, but these situations were judged to cause the most error in matching murrelet counts with appropriate watershed areas. I omitted data from Lemmen's Inlet on Meares Island (LI) and Cow Bay on Flores Island (CB) because each station had only 1 survey, and the watersheds were not clearly defined. Bedwell and Ursus valleys were treated separately (see above). The habitat measures for the 18 adjusted areas are given in Appendix 1.

I used SPSS 10.0 for statistical analyses. Percentages were arcsine transformed before analysis (Zar 1996:282). I compared the 2 phases of the breeding season and 2 weather categories using the paired *t*-test. I used repeated-measures ANOVA for comparisons among years and treated each station as a separate subject and mean counts within each year as the within-subject factor. Both paired *t*-tests and repeated measures ANOVA emphasize the differences between repeated counts (i.e., counts made at the same station at different times), rather than the values or means of the counts themselves (Zar 1996), which differed greatly among stations. I could not use multivariate ANOVA (which could simultaneously test weather, seasonal, and annual effects) because most cells were either empty or had small samples, and large differences occurred in counts among the stations that masked other effects. The Tukey test (Zar 1996) was used for post hoc tests among variables found to have significant differences in ANOVA. I calculated the annual coefficient of variation (CV = 100 × SD/mean) for those stations sampled more than once per year and used paired *t*-tests to compare the CV of dawn and dusk counts.

RESULTS

Birds and Bats Likely to be Confused with Marbled Murrelets

Loons, mergansers, scoters, shorebirds, gulls, and crows were the most common birds of similar size to murrelets (Table 1). Comparison of

Table 1. Mean values of the maximum daily counts of birds that might be confused with marbled murrelets on radar screens seen at the 18 radar stations in 1996–1998.

Species	Mean no. birds seen per day	Occurrence per station %
Loons (*Gavia immer* and *G. stellata*)	1.3	94
Common merganser (*Mergus merganser*)	5.1	89
Surf scoter (*Melanitta perspicillata*)	4.3	28
Other ducks	1.0	28
Bald eagle (*Haliaeetus leucocephalus*)	1.7	100
Merlin (*Falco columbarius*)	0.1	28
Shorebirds (Charadrii and Scolopacidae)	1.2	72
Mew gulls (*Larus canus*)	5.3	100
Other gulls (*Larus* spp.)	0.4	56
Band-tailed pigeon (*Columba fasciata*)	0.5	56
Belted kingfisher (*Cyryle alcyon*)	0.2	56
Common nighthawk (*Chordeiles minor*)	0.1	28
Northwestern crow (*Corvus caurinus*)	5.3	94
Common raven (*Corvus corax*)	1.0	89

Table 2. Ground speeds (km/h) of flying birds and bats recorded with radar in Clayoquot Sound. These measurements were made with wind speeds averaging less than 13 km/h (Beaufort scale <3), and in most cases during calm conditions.

Species	Mean	Range	*n*
Marbled murrelet: incoming	66	35–139	424
Marbled murrelet: outgoing[a]	105	42–166	487
Marbled murrelet: circling	69	35–101	21
Common loon	66	60–77	3
Common merganser	59	48–72	6
Mew gull	34	24–48	18
Bald eagle	37	35–42	6
Common nighthawk	48	–	1
Vaux's swift (*Chaetura vauxi*)	22	14–27	12
Violet-green swallow	26	21–33	15
Northwestern crow	32	24–48	12
Bats (unidentified species)	21	8–38	29

[a] Outgoing marbled murrelets, descending from above the treetops to sea level, flew significantly faster than incoming or circling birds (Burger 1997).

flight speeds was an important means of separating the fast-flying murrelets from most other common birds and bats (Table 2).

Dawn and Dusk Counts

Counts of marbled murrelets during dusk surveys averaged 33.6% (SD = 35.9%, $n = 127$) of the counts on the following dawn surveys. Dusk counts exceeded the following day's dawn counts in only 5 of 127 survey days. The annual CV of counts at each station was significantly higher for dusk than dawn counts in 1996 (paired *t*-test, $t_{10} = 5.09$, $P < 0.001$), 1998 ($t_7 = 3.77$, $P = 0.007$) and in all years combined ($t_{15} = 2.52$, $P = 0.024$), but no difference occurred in 1997 ($t_{13} = 0.17$, $P = 0.87$). I therefore used dawn surveys to estimate the total numbers of murrelets per watershed, but used both dawn and dusk surveys to examine seasonal and annual variations and to rank the watersheds.

Incoming and Outgoing Flights

At dawn, incoming numbers were higher than outgoing numbers in 90% of all surveys ($n = 150$, all years pooled). When outgoing counts were higher these were generally surveys with few birds (often late in the season) and the differences between incoming and outgoing were usually less than 10%. For consistency, I used incoming birds for all dawn counts. By contrast, outgoing counts exceeded incoming in 53% of dusk surveys ($n = 138$, all years pooled). Accordingly, I used the maximum of either incoming or outgoing birds for dusk counts.

Variations in the Timing of Dawn Detections

Typically, incoming murrelets showed a strong, unimodal distribution with most birds moving inland before sunrise (Fig. 2A). Most murrelets evidently made a single entrance to the watershed at dawn to visit the nest or undertake other activities such as nest prospecting. On a few mornings, however, evidence showed that murrelets made repeated visits. An obvious example is shown in Fig. 2B. On this morning, the day after the sample shown in Fig. 2A and at the same station, I counted 39% of the incoming birds after sunrise. On another occasion at the same station, I recorded 2 pulses of incoming birds after sunrise (Fig. 2C). These post-sunrise pulses were probably due to some birds making second or third inland trips, following the initial pre-sunrise entrance. The timing between peaks (approximately 60 min in the examples from the Moheya Valley) was consistent with the time required for a murrelet flying at 70 km h^{-1} to make a round trip (approximately 40 km in the case of Moyeha Valley) between feeding sites and an inland nest, with some time remaining to catch a fish or deliver a fish to a chick.

Surveys with a high proportion of post-sunrise counts were rare (Fig. 3): 61% of surveys had <5% of the incoming birds after sunrise, and 92% had <20% after sunrise. In the examples shown (Fig. 2), post-sunrise visits occurred on overcast, misty mornings, but they were not restricted to such weather and, conversely, such weather did not always produce high post-sunrise counts. I found no significant effect of weather on the percentage of incoming birds counted after sunrise, with data from all years pooled (Fig. 4; ANOVA using arcsine transformed percentages, $F_{2;\ 142} = 1.430$, $P = 0.243$), or with each year tested separately ($P > 0.30$ in each case). Since the radar was ineffective in heavy drizzle or rain, I could not test whether significant numbers of murrelets came in after sunrise under these conditions.

High post-sunrise counts varied seasonally and were most likely adults making repeated nest visits to feed chicks. Of 39 surveys in which >10% of the incoming birds were recorded after sunrise, 85% occurred after 1 June when chicks were expected. Nevertheless, even during chick-rearing most surveys showed little or no post-sunrise influx, and

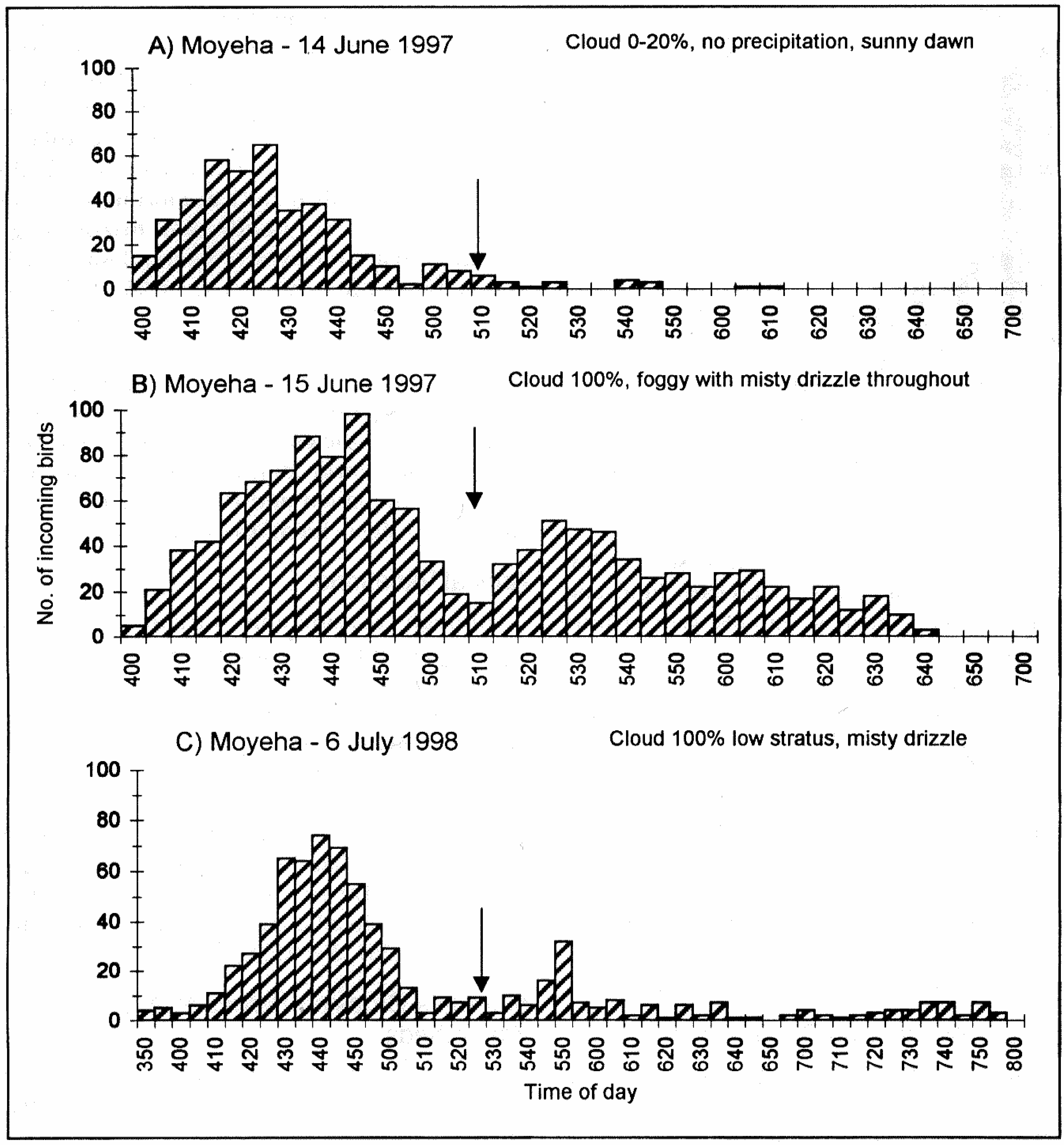

Fig. 2. The timing of incoming flights by murrelets during 3 dawn surveys made at the Moyeha station, plotted in 5 min intervals. The first graph (A) indicates the pattern most often seen in dawn surveys, with few birds reported after sunrise. Graphs B and C illustrate less common patterns, with 1 (B) or 2 (C) pulses of incoming birds after sunrise. Arrows indicate sunrise times.

with all years pooled, there was no significant correlation with date (arcsine transformed percentages, Pearson coefficient, $r = 0.071$, df = 144, $P > 0.05$). Within each year, post-sunrise influx showed no correlation with date in 1996 ($r = -0.248$, $P = 0.074$, $n = 51$) and 1997 ($r = 0.112$, $P = 0.407$, $n = 56$), but was positively correlated with date in 1998 ($r = 0.749$, $P < 0.001$, $n = 38$). On most mornings, murrelets made only a single pre-sunrise visit to the nest, even when feeding chicks. To avoid possible double counting, I used only pre-sunrise counts of incoming murrelets in all subsequent analyses of dawn surveys.

Seasonal Trends

Considerable variability occurred in counts through the season in dawn and dusk surveys, but a few obvious patterns are apparent (Fig. 5). At dawn, low counts occurred consistently after mid-July, at the end of breeding, and in early May 1998, during incubation. Seasonal maxima (100% values) in dawn surveys at each station occurred

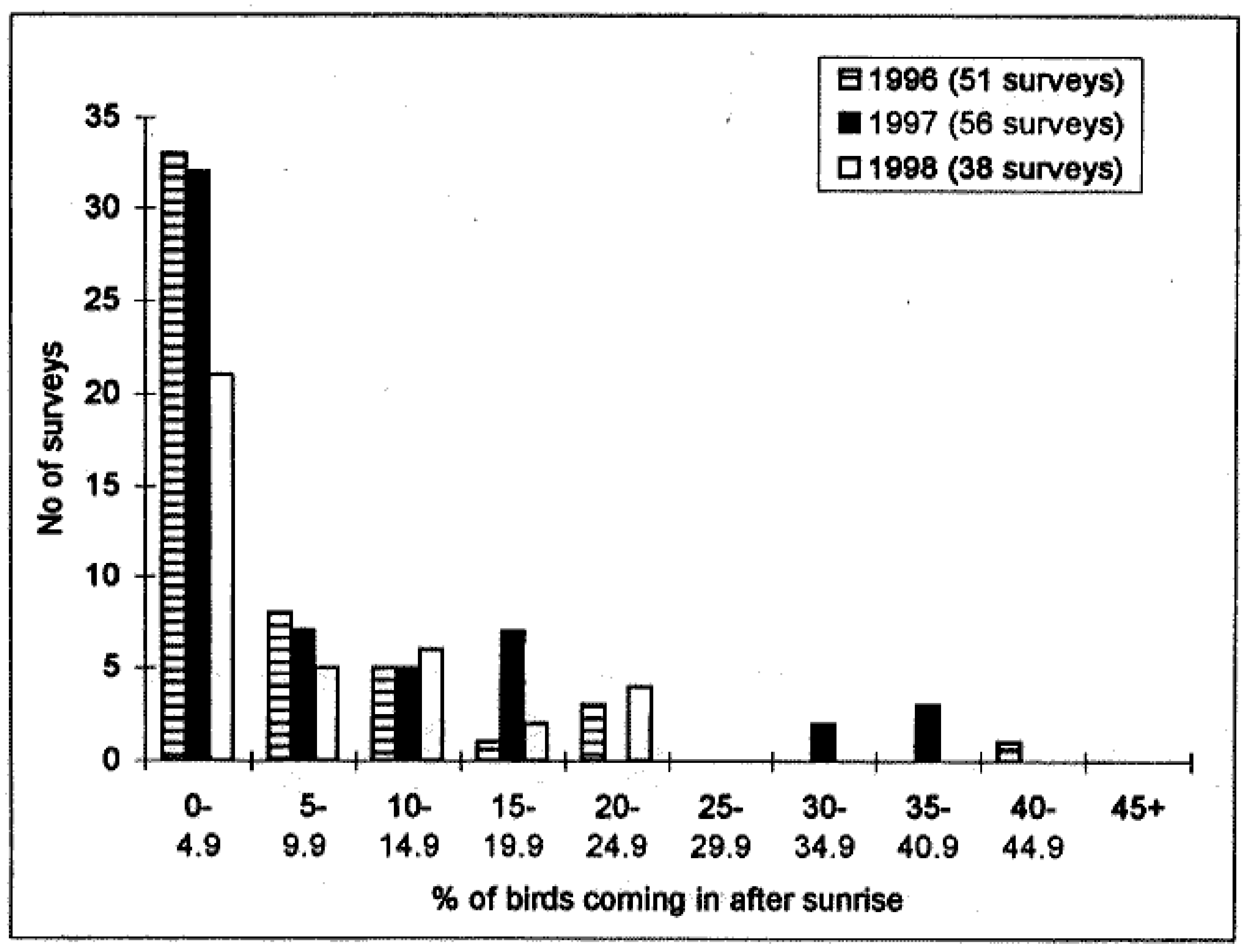

Fig. 3. Frequency distribution of post-sunrise counts of incoming murrelets in 1996–1998, plotted as a percentage of the total count per dawn survey.

from May through mid-July. For dusk surveys, low counts were common in May and early June, and maximum counts at most stations were in June and July.

To minimize seasonal variations, I used the period 15 May through 16 July as the core sampling period. Most stations were sampled on 2 visits within the core period, allowing pairwise comparisons of early (15 May–15 Jun) and late (16 Jun–16 Jul) periods. For dawn surveys, I found no significant differences between these periods (Table 3). For dusk surveys, early counts tended to be higher than late ones in 1996, but no differences occurred in the other 2 years or in the pooled data from all 3 years (Table 3).

Effects of Weather on Radar Counts

I tested the effects of weather by comparing counts of marbled murrelets from surveys with varying weather conditions at the same station within the core period of the same year (Fig. 6). Pre-sunrise counts were on average 1.4 times higher on cloudy or drizzly/foggy days than on clear days (paired *t*-test, $t_{15} = 2.94$, $P = 0.01$), but no difference occurred between cloudy and drizzly/foggy days ($t_7 = 1.26$, $P = 0.25$). Dusk counts were 2.8 times higher on cloudy than clear days (paired *t*-test, $t_{17} = 2.09$, $P = 0.05$), but data were insufficient to test the effects of precipitation, which was rare at dusk.

To include more surveys in a more indirect test, I compared the effects of cloud and precipitation on the survey counts expressed as a percentage of the highest count for that station in that season. I included only stations visited more than once per season. With all years pooled, I found a significant increase in the mean percentage count with increasing cloud and precipitation in pre-sunrise counts (1-way ANOVA with arcsine transformed percentages, $F_{2;\,100} = 3.68$, $P = 0.03$), but not at dusk ($F_{2;\,88} = 0.542$, $P = 0.58$). Post hoc Tukey's test revealed that the difference was due to higher counts on cloudy than clear mornings, but no difference between cloudy and drizzly/foggy mornings. Within the years, the trend was significant at dawn only in 1997 ($F_{2;\,36} = 6.96$, $P = 0.003$), but not in 1996 or 1998 ($P > 0.05$), and was not significant at dusk in any year ($P > 0.05$).

The major effect of weather on counts was due to cloudiness rather than precipitation. I therefore controlled the effects of weather when comparing counts made during different years, but combined the cloud and drizzle/fog categories (hereafter called cloud/drizzle/fog).

Annual Variations

Although considerable variation occurred among years for counts at some stations (Fig. 7), I found no significant difference among years in mean pre-sunrise counts on cloudy mornings (repeated-measures ANOVA, $F_{2;\,10} = 0.479$, $P = 0.633$) or in all dawn surveys, regardless of weather ($F_{2;\,16} = 0.575$, $P = 0.574$). I had insufficient data to test clear mornings. I found no significant differences in mean dusk counts on clear ($F_{2;\,8} = 1.352$, $P = 0.312$) or cloudy ($F_{2;\,4} = 0.008$, $P = 0.992$) days, or in all evenings regardless of weather ($F_{2;\,16} = 1.557$, $P = 0.238$).

Murrelets Crossing Ridges to Adjacent Watersheds

Some murrelets counted by radar at watershed mouths crossed low ridges into adjacent water-

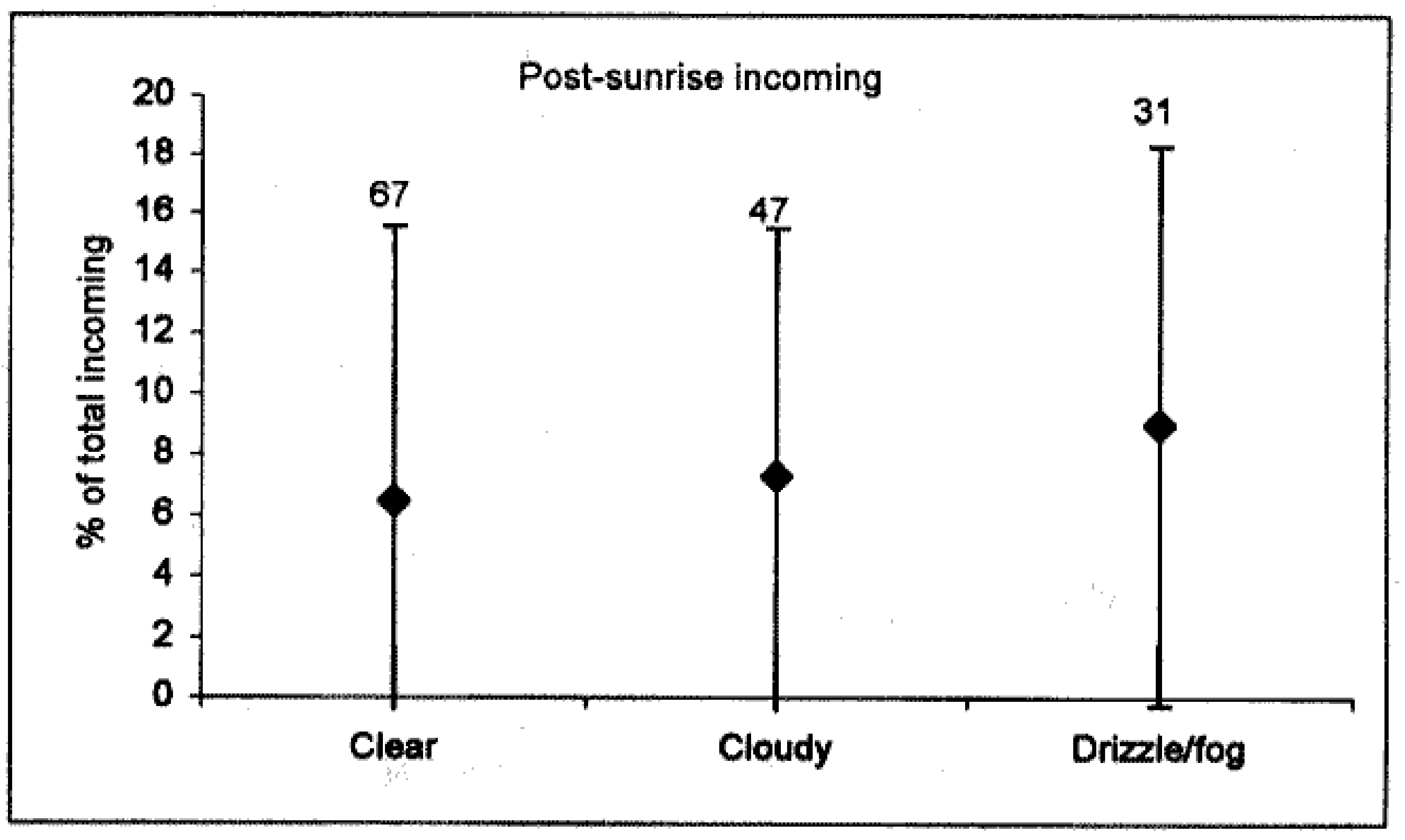

Fig. 4. Mean (± SD) percentage of incoming birds recorded after sunrise on clear (<80% cloud cover), cloudy (80% cloud cover, no precipitation) or drizzly/foggy mornings. The number of dawn surveys in each category is shown. Data are pooled from all years.

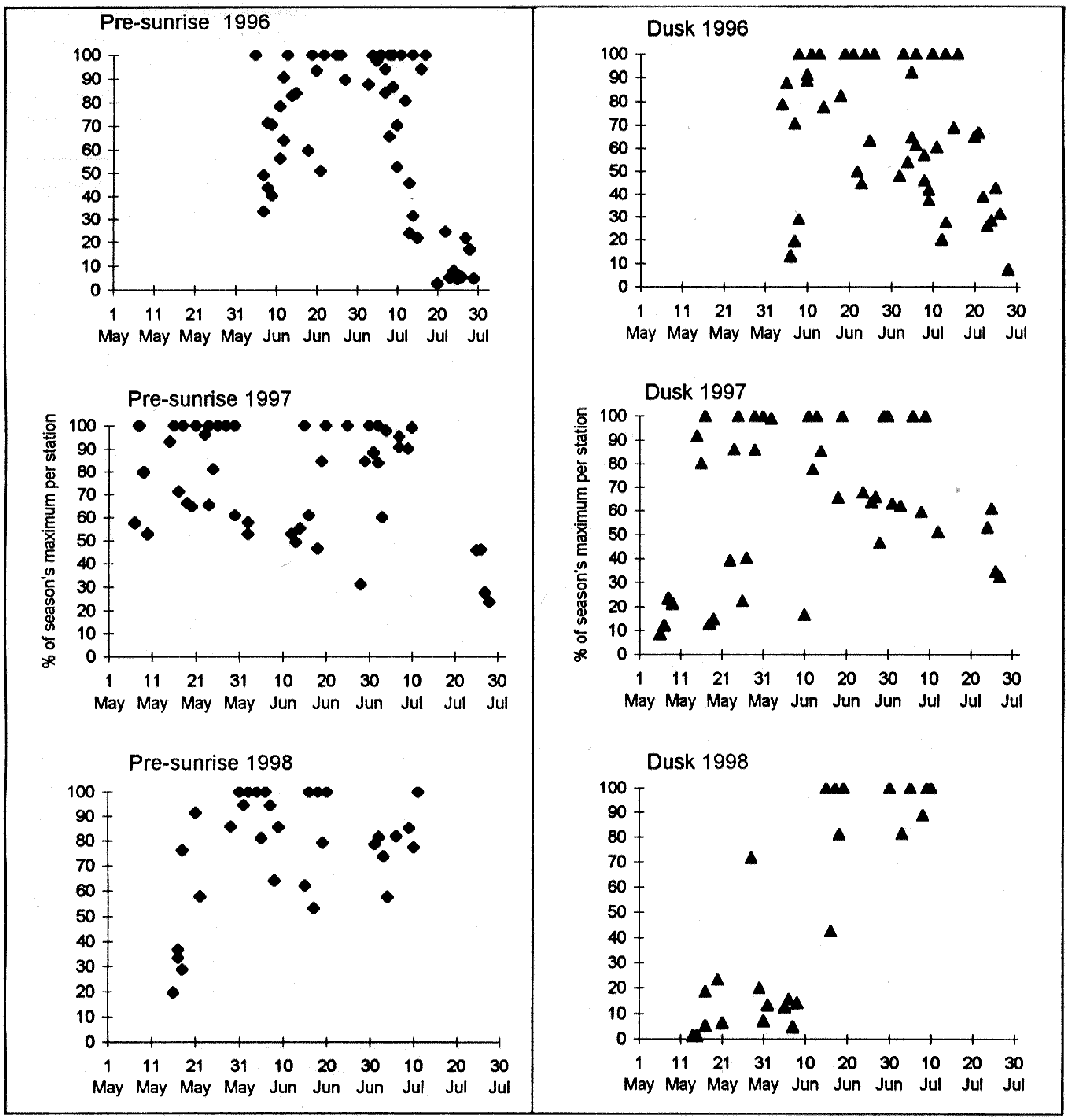

Fig. 5. Seasonal variations in counts of murrelets at dawn (left graphs) and dusk (right). Counts are plotted as the percentage of the maximum count in each year for each station. Only stations visited 2 or more times per year were included.

sheds. Murrelets crossed from the Watta Valley to the East Megin Valley (Fig. 1) across a 250-m-high ridge (S. Hughes, Arbonaut Access Inc., personal communication). Using a radar unit stationed near 2 mountain passes (500 and 600 m high) in the upper Kennedy Valley, my team tracked small numbers of murrelets (3–20 and 0–14 per site, respectively, in 4 surveys) heading towards the passes, and some of these birds likely crossed to the adjacent valley. Murrelets regularly took shortcuts across 200-m-high ridges near the valley mouths to enter Pretty Girl and Bulson valleys, but these birds were detected by radar and included in the counts for these valleys.

Assessing Murrelet Populations and Relative Importance of Watersheds

For both dawn and dusk counts, I calculated the overall mean of annual mean counts and the mean of the annual maximum counts per watershed (Table 4). All 4 measures were significantly intercorrelated ($r > 0.74$, $P < 0.01$ in each case) and gave similar rankings of watershed populations, but since not all birds entered watersheds at dusk, dawn counts gave higher and less variable estimates of the total populations. High counts were consistently made in Moyeha, Watta, Megin, Clayoquot River, Kennedy River, Bedwell–Ursus, and Bulson watersheds in all years (Fig. 7), and collectively these areas included >60% of all the Clayoquot murrelets (Table 4).

Relationships Between Murrelet Counts and Habitat Features

I compared dawn counts with a range of macrohabitat measures derived from GIS databases (Table 5) within 18 watersheds (Appendix 1). Both Dawnmean and Dawnmax counts were considered here because both measures have been used in other studies. As explained in the methods, I omitted the Cow Bay and Lemmen's Inlet data from this analysis, treated the Bedwell and Ursus valleys separately, and adjusted the catchment areas of a few watersheds to account for likely flight paths across low ridges.

Murrelet counts were significantly correlated with the total area of watersheds, and several other habitat measures (Table 6). Because many of the habitat variables showed significant correlations with total watershed area (Appendix 2), I controlled for this variable when testing correlations. After controlling for total watershed area, the correlations between murrelet counts and areas of original forest, alpine, high-elevation mature forest (Mathigh) and mid- to high-elevation biogeoclimatic subzones (Maturevm2 and Maturemm1) were no longer significant. By contrast, negative correlations with logged and immature areas became statistically significant, and positive correlations with total mature forest (Mature), mature forest below 600 m (Matlow), and the mature low-elevation CWHvm1 biogeoclimatic subzones (Maturevm1) remained significant (Table 6).

Stepwise multiple regression models showed the combined effects of important habitat measures, and yielded the following equations:

Dawnmean = 69.169 + 0.033Maturevm1 − 0.089Logimm + 0.049Maturevm2 (adjusted R^2 = 0.913, $P < 0.001$);

Dawnmax = 110.914 + 0.031Maturevm1 − 0.100Loggimm + 0.060Maturevm2 (adjusted R^2 = 0.860, $P < 0.001$).

Table 3. Comparison of counts of marbled murrelets made at stations sampled in each of 2 time periods. Dawn surveys included only pre-sunrise counts and dusk surveys the maximum of incoming or outgoing per survey. Counts were averaged if there was more than 1 survey at a station per period.

		Dawn surveys[a]		Dusk surveys[b]	
Year	Station	15 May–15 Jun	16 Jun–16 Jul	15 May–15 Jun	16 Jun–16 Jul
1996	Atleo	48	73	55	43
	Bedwell–Ursus	404	384	82	66
	Bulson	287	322	119	55
	Cypre	22	53	6	26
	Megin	412	442	178	137
	Moyeha	233	304	253	169
	Tranquil	172	87	36	10
1997	Bedwell–Ursus	250	373	–	–
	Bulson	245	346	74	157
	Clayoquot River	347	609	102	76
	Cypre	69	32	–	–
	Kennedy	–	–	130	102
	Hesquiat Point	106	103	–	–
	Megin	526	478	69	219
	Moyeha	469	755	–	–
	Pretty Girl	280	244	27	18
	Tofino Creek	–	–	57	29
	Tranquil	211	228	102	61
	Watta	524	496	136	126
1998	Bedwell–Ursus	303	538	41	613
	Bulson	353	373	18	151
	Clayoquot River	246	252	7	34
	Kennedy	206	215	38	48
	Moyeha	649	545	27	200
	Pretty Girl	210	168	6	45
	Sydney	207	168	–	–
	Watta South	21	48	10	13

[a] Paired *t*-tests (2-tailed): 1996: $t = 0.633$, df = 6, $P = 0.058$; 1997: $t = 1.601$, df = 9, $P = 0.144$; 1998: $t = 0.408$, df = 7, $P = 0.696$; all years pooled: $t = 1.664$, df = 24, $P = 0.109$.

[b] Paired *t*-tests (2-tailed): 1996: $t = 2.464$, df = 6, $P = 0.048$; 1997: $t = 0.471$, df = 7, $P = 0.651$; 1998: $t = 1.785$, df = 6, $P = 0.125$; all years pooled: $t = 1.283$, df = 21, $P = 0.214$.

These combined variables explained 91% and 86%, respectively, of the variability in Dawnmean and Dawnmax counts, although most of the variability (70% and 64%, respectively) was explained by Maturevm1 alone. Several measures of old-growth area (Mature, Matlow, Maturevm1, Maturevm2) combined with areas of logged and immature forest (Logimm) produced multiple regressions with similar predictive power to the equations above (R^2 values 0.76–0.91).

A simple linear regression of murrelet numbers plotted against Matlow was the most parsimonious and practical model. The regression was plotted through the origin to deal with small habitat areas. The resultant equations were:

Dawnmean = 0.0653 × Matlow (SE ± 0.005 × Matlow; $R^2 = 0.898$, df = 17, $P < 0.001$);

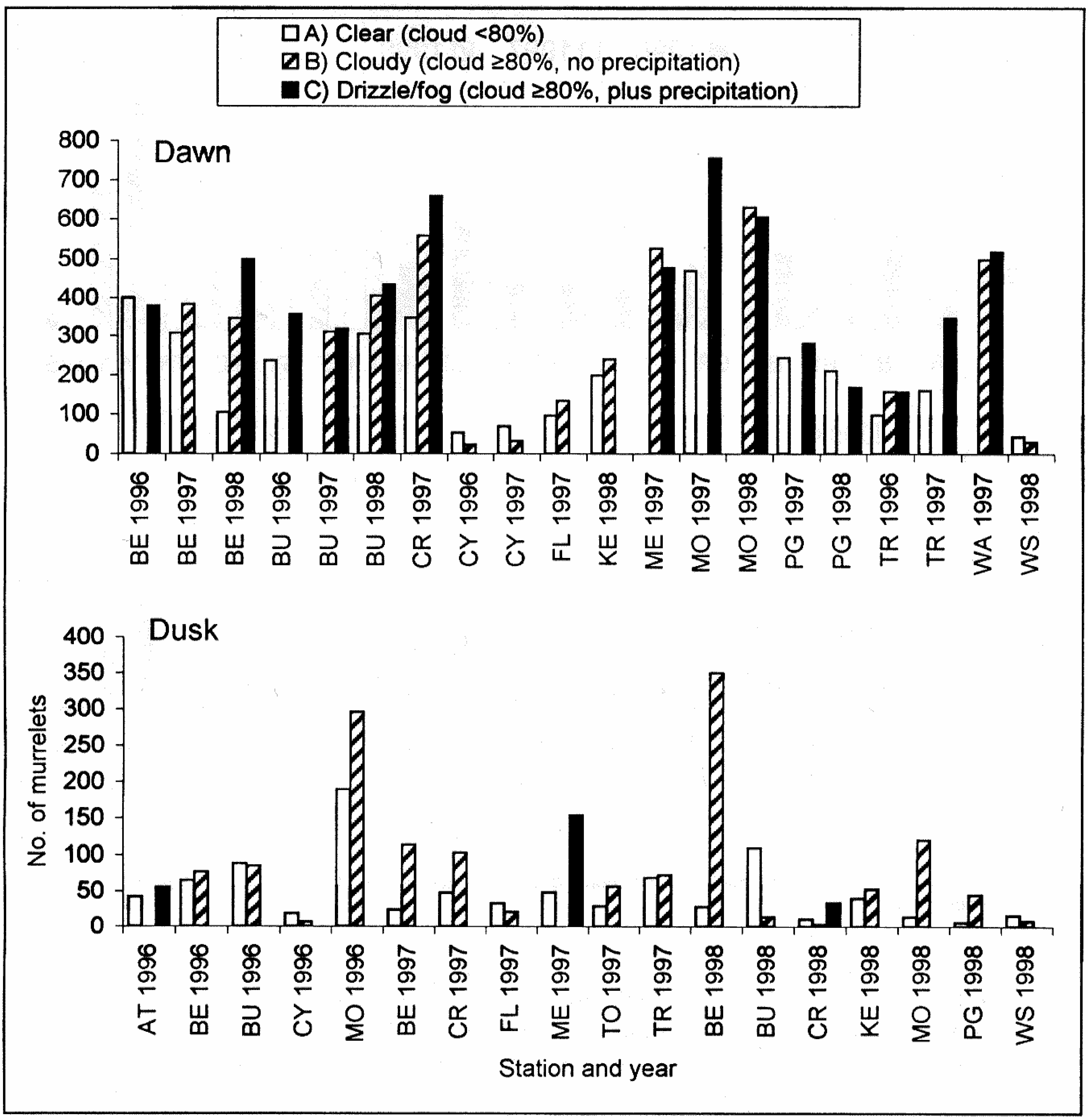

Fig. 6. Effects of increasing cloud and precipitation on the numbers of murrelets counted at dawn (upper graph) and dusk (lower). Data from days with differing weather conditions within the period 15 May through 16 July were grouped by station and year. See Appendix 1 for the codes of each station.

Dawnmax = 0.0770 × Matlow (SE ± 0.006 × Matlow; $R^2 = 0.892$, df = 17, $P < 0.001$), with Matlow measured in ha. The R^2 values differ from those calculated from R values in Table 6 because of the effects of forcing the regressions through the origins.

The effects of clearcut logging were evident when mean dawn counts were plotted against forest areas (Fig. 8). When the total area of original forest was considered, including those portions recently logged or immature, the watersheds formed a close linear pattern (Fig. 8A), with the exception of 3 large watersheds (Cypre, Bedwell, and Kennedy) that had lost large portions of the original old-growth forest (38%, 20%, and 17%, respectively), and disproportionately large amounts of low-elevation old-growth <600 m (51%, 35%, and 29%, respectively). Two smaller watersheds, Atleo and Tranquil Creek, which had lost 35% and 20% of the original old-growth forest (45% and 35% of low-elevation forest, respectively) did not show the deviation from the linear trend. The deviations persisted when dawn counts were compared with total area of remain-

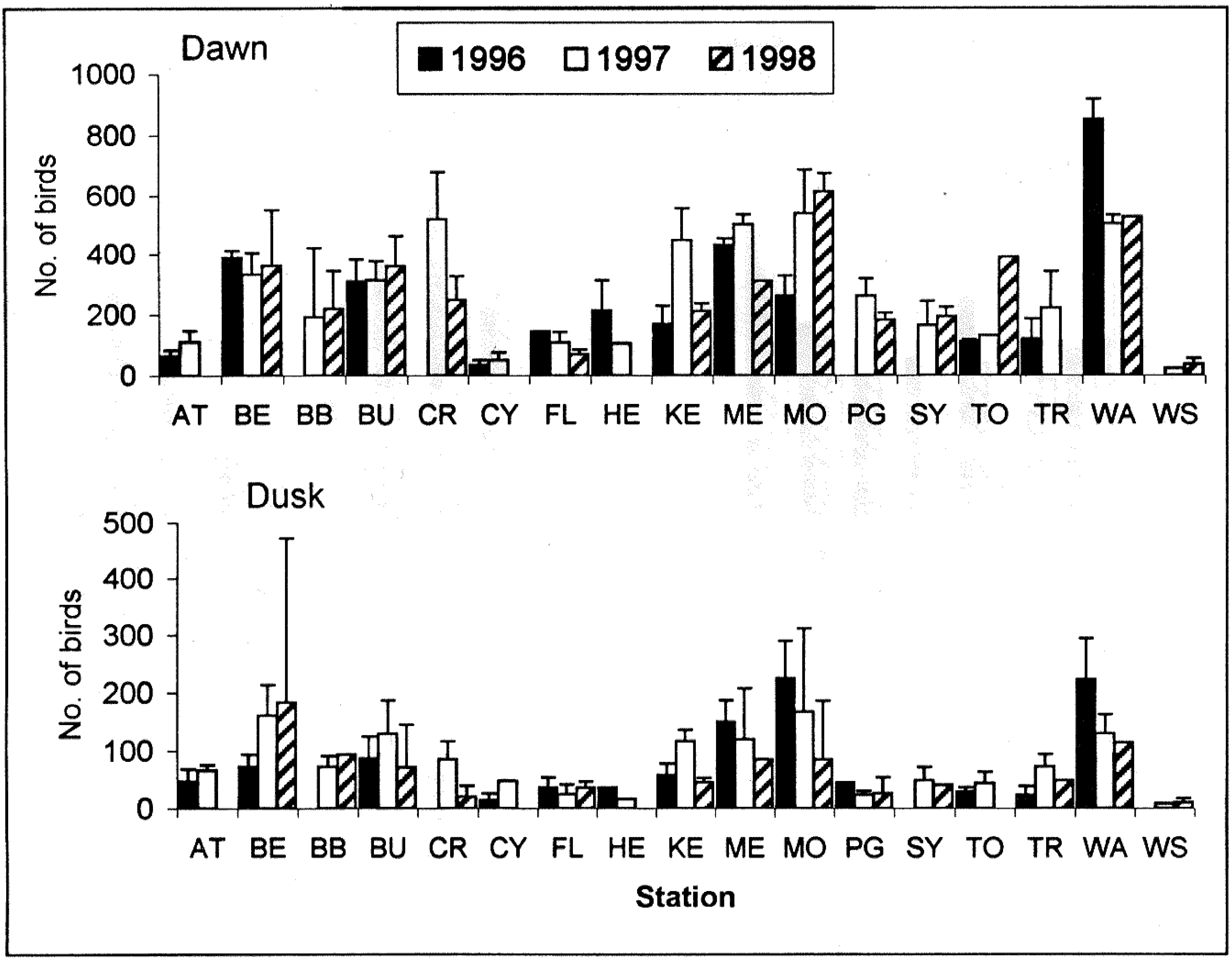

Fig. 7. Annual mean (± SD) count of murrelets at dawn (upper graph) and dusk (lower) at each station in 1996–1998. See Appendix 1 for the codes of each station.

ing mature forest at all elevations (Fig. 8B) but disappeared when compared with remaining low-elevation old-growth (Fig. 8C). The dichotomous grouping evident in the latter plot, apparent as 2 separate linear groups, could not be explained by differences in the proportions of any of the habitat variables considered here (Mann-Whitney tests for all variables listed in Table 5, $P > 0.19$ in each case). Finally, mean counts were poorly predicted from remaining areas of high-elevation mature forest (Mathigh), which was considered because some nests have been found above 800 m in Clayoquot Sound (Fig. 8D, Table 6).

DISCUSSION

Factors Affecting Radar Counts of Murrelets

Radar counts of marbled murrelets are becoming common throughout the species' range (Cooper and Hamer 2000), but published analyses of the factors affecting counts are few and incomplete (Hamer et al. 1995, Burger 1997, Cooper et al. 2001). This study revealed some of the strengths and limitations of radar as a tool for watershed-level inventory and habitat analysis. Counts were affected by time of day, flight direction (incoming or outgoing), weather, seasonal variations, occasional multiple visits by birds at dawn, and the possibility of birds crossing from 1 watershed to another. Similar effects are likely at other locations (Cooper et al. 2001). The effects of these factors need to be tested and radar counts adjusted where necessary.

Confusion with Other Species.—In general, it was easy to separate images of murrelets from those of most other birds or bats, on the basis of speed, flight path, size of image, and pre-dawn activity (see also Hamer et al. 1995, Burger 1997, Cooper et al. 2001). Murrelets flew faster, had more direct flight, and produced larger images than most other birds and all bats. During dawn surveys, the air was often calm and wind speeds <13 km · h^{-1} (Beaufort scale <3). Wind was therefore

Table 4. Means and SD of all counts, means of maximum counts, and percentage of total counts at 19 watersheds in Clayoquot Sound in 1996–1998.

	Dawn surveys (pre-sunrise count)						Dusk surveys					
Station	Overall mean	SD	*n*[a]	%	Mean of max.[b]	% max.	Overall mean	SD	*n*[a]	%	Mean of max.[b]	% max.
Atleo	87	33	2 (6)	1.9	118	2.1	56	13	2 (6)	4.5	69	3.9
Bedwell–Ursus	361	28	3 (11)	7.8	441	8.0	139	59	3 (11)	11.2	303	17.2
Boat Basin	206	20	2 (4)	4.5	331	6.0	83	15	2 (4)	6.7	89	5.0
Bulson	326	29	3 (14)	7.1	412	7.4	96	30	3 (12)	7.8	158	9.0
Clayoquot River	385	193	2 (7)	8.3	494	8.9	52	45	2 (7)	4.2	75	4.2
Cow Bay	259	–	1 (1)	5.6	259	4.7	30	–	1 (1)	2.4	30	1.7
Cypre	42	11	2 (7)	0.9	63	1.1	31	23	2 (7)	2.5	40	2.3
Flores #6	108	39	3 (6)	2.3	120	2.2	32	6	3 (8)	2.6	45	2.5
Hesquiat Point	160	77	2 (5)	3.5	196	3.5	26	14	2 (2)	2.1	26	1.5
Kennedy	276	151	3 (9)	6.0	334	6.0	73	38	3 (7)	5.9	85	4.8
Lemmen's Inlet	83	–	1 (1)	1.8	83	1.5	21	–	1 (1)	1.7	21	1.2
Megin	415	97	3 (6)	9.0	430	7.8	118	33	3 (7)	9.5	160	9.1
Moyeha	472	186	3 (12)	10.2	596	10.8	159	70	3 (10)	12.8	270	15.3
Pretty Girl	222	56	2 (7)	4.8	260	4.7	31	11	3 (6)	2.5	39	2.2
Sydney	180	20	2 (5)	3.9	225	4.1	44	6	2 (3)	3.6	52	2.9
Tofino Creek	212	155	3 (4)	4.6	213	3.8	36	10	2 (4)	2.9	46	2.6
Tranquil	172	71	2 (8)	3.7	268	4.8	47	25	3 (9)	3.8	63	3.6
Watta	628	194	3 (6)	13.6	650	11.7	155	59	3 (6)	12.5	182	10.3
Watta South	30	10	2 (6)	0.7	45	0.8	9	2	2 (4)	0.7	12	0.7
Totals	4,624	–	–	100.0	5,537	100.0	1,238	–	–	100.0	1,765	100.0

[a] Sample size is number of annual means; the number of surveys in all years is shown in parentheses.

[b] Mean of annual maximum number of birds counted.

Table 5. Codes and descriptions of parameters used in comparing numbers of marbled murrelets and habitat parameters in watersheds in Clayoquot Sound.

Code	Parameter description
Marbled murrelet counts	
Dawnmean	Mean of the annual mean count of murrelets at dawn for 1996–1998.
Dawnmax	Mean of the annual maximum count of murrelets at dawn for 1996–1998.
Habitat attributes per watershed	
Alpine	Area of alpine meadows and scrub (ha).
Distfeed	Distance from the watershed mouth to the nearest foraging aggregation (km).
Imm	Area of immature forest 20–140 years old (ha).
Logged	Area of recently logged forest <20 years old (ha).
Logimm	Combined area of logged and immature forest (ha).
Mathigh	Area of all mature forest above 600 m elevation (ha).
Matlow	Area of all mature forest below 600 m elevation (ha).
Mature	Area of mature forest >140 years old (ha).
Maturemm1	Area of mature forest in the MHmm1 biogeoclimatic subzone (ha).
Maturevh1	Area of mature forest in the CWHvh1 subzone (ha).
Maturevm1	Area of mature forest in the CWHvm1 subzone (ha).
Maturevm2	Area of mature forest in the CWHvm2 subzone (ha).
Origforest	Area of original forest (existing mature, logged, and immature; ha).
Totarea	Total area of the watershed (ha).

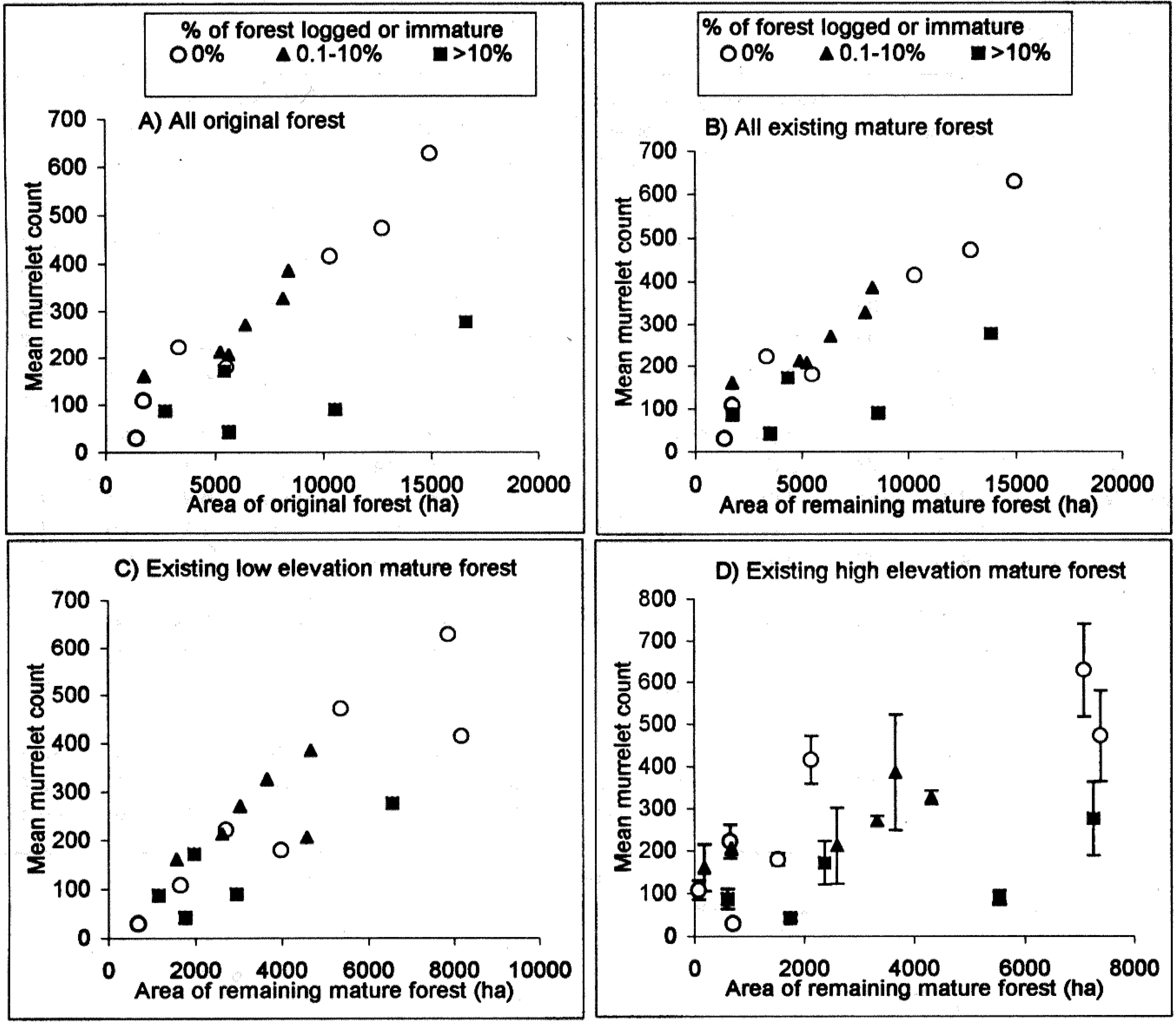

Fig. 8. Mean counts of murrelets (mean of annual mean counts) at 18 watersheds in Clayoquot Sound plotted against various measures of forest area, including: area of all original forest at all elevations, including mature, recently logged, or immature forest at the time of the study (A); area of mature forest remaining at the time of the study at all elevations (B); area of mature forest remaining in low elevations <600 m (C); and area of mature forest remaining at high elevations >600 m (D). Watersheds were labeled according to the proportion of original forest which was recently logged or immature at the time of the study (see legend). For clarity, error bars (± SE) are shown in only 1 graph.

unlikely to have affected flight speeds sufficiently to cause confusion between murrelets and slower species. Concurrent visual observations improved the accuracy of radar counts by identifying confounding species, such as mergansers.

Gulls were present at all stations (but not on all days), but their slow, meandering flight was quite different from that of murrelets. Scoters and other sea ducks seldom flew and then usually remained over the water. Shorebirds were usually in distinct flocks and kept to the shore. Band-tailed pigeons (*Columba fasciata*), which might be confused with murrelets on radar screens (Hamer et al. 1995, Cooper et al. 2001), occurred in small numbers at about half the Clayoquot stations. Swallows, swifts, and bats were excluded by their smaller images, and slower, more meandering flight paths than murrelets.

The species most likely to be confused with murrelets was the common merganser (*Mergus merganser*), which flew at similar speeds (Table 2), produced similar-sized radar images, and also crossed from the ocean into the lower valleys. A few mergansers might inadvertently have been counted as murrelets, but mergansers were rare (Table 1), and usually could be excluded because they were seen or heard by observers or landed on the estuary instead of proceeding up the val-

Table 6. Correlations and partial correlations (controlling for total watershed area) between radar counts of marbled murrelets (Dawnmean and Dawnmax) and habitat measures at 18 watersheds in Clayoquot Sound. See Table 5 for habitat codes.

	Uncontrolled (Pearson correlation)		Controlled for total area (partial correlation)	
Habitat measure	Dawnmean	Dawnmax	Dawnmean	Dawnmax
Total watershed area	0.704**	0.694**	–	–
Distance to feeding aggregation	0.323	0.318	0.004	0.003
Forest age				
Immature (20–140 yr)	−0.196	−0.213	−0.757**	−0.767**
Logged (<20 yr)	−0.323	−0.298	−0.646**	−0.601*
Logimm (0–140 yr)	−0.344	−0.332	−0.862**	−0.828**
Mature (>140/250 yr)	0.822**	0.803**	0.845**	0.771**
Original forest	0.713**	0.696**	0.160	0.094
Elevation of mature habitat				
Alpine	0.560*	0.570*	−0.158	−0.103
Mathigh (>600 m)	0.677**	0.667**	−0.008	−0.002
Matlow (<600 m)	0.824**	0.796**	0.620**	0.566*
Biogeoclimatic zone				
Maturevh1 (exposed low)	−0.415	−0.386	−0.204	−0.162
Maturevm1 (<600 m)	0.850**	0.813**	0.674**	0.600*
Maturevm2 (600–900 m)	0.686**	0.685**	0.084	0.120
Maturemm1 (>900 m)	0.511*	0.504*	−0.271	−0.265

*$P < 0.05$

**$P < 0.01$

ley. Overall, confusion with other flying birds or bats was a negligible source of error in this study.

Dawn versus Dusk Counts.—Dawn counts of murrelets were almost always higher and less variable than those at dusk. Cooper et al. (2001) found similar results on the Olympic Peninsula. Observations at murrelet nests showed that nearly all incubation exchanges and about 60% of meal deliveries to chicks occurred at dawn (Nelson and Hamer 1995). Audiovisual surveys to detect presence and occupancy of murrelets in forest stands are traditionally done at dawn (Evans et al. 2000). I did not document flights through the day between dawn and dusk using radar, but visual observations (personal observations) and nest-watches (Nelson and Hamer 1995) suggest that these are rare. Elsewhere on Vancouver Island (Carmanah and Walbran valleys), all-night radar watches revealed no nocturnal murrelet activity between the known peaks at dusk and dawn (personal observations).

Although dawn radar counts are the most reliable measure of total watershed populations, dusk surveys provided useful supporting information, particularly when time constraints or rain limited the number of dawn surveys at each station. In Clayoquot Sound, only 7% of dusk surveys were in drizzle or fog, compared to 33% of dawn surveys (excluding those abandoned because of heavy rain). Dusk surveys provided similar rankings of the relative importance of the watersheds sampled and were useful for showing seasonal variations in activity.

Incoming versus Outgoing Counts.—Counts of incoming murrelets were almost invariably higher than outgoing at dawn, but not at dusk. This difference in detectability probably was due to effects of light intensity on the birds' altitude and flight paths. Birds coming in from the sea in the reduced visibility of pre-dawn twilight evidently flew well above the trees to avoid collisions, and were therefore readily detected by radar. Murrelets usually returned to sea after sunrise, and with better visibility, tended to fly lower, making them less likely to be detected by radar. Visual observations confirmed that many outgoing murrelets flew at or below treetop levels, sometimes along creek beds. The situation was reversed in the evening, making it more likely to detect the higher-flying outgoing birds. Cooper et al. (2001) concluded that incoming (landward) counts were more reliable than outgoing counts on the Olympic Peninsula.

Repeated Entries.—Multiple entries by some of the birds might obviously cause overestimates of the numbers per watershed. Murrelet chicks at 10 nests were fed, on average, 3.2 times per day (range 1–8), involving both parents and including dawn and dusk feeds (Nelson and Hamer 1995). This suggests that adults with a chick usually make a single nest visit per morning. Only a single visit is needed for an incubation exchange, which occurs at dawn (Nelson and Hamer 1995). Although multiple dawn visits were uncommon, their occurrence would seriously bias counts. To avoid this I restricted analysis to pre-sunrise counts. Sunrise is a convenient, seasonally adjusted and biologically meaningful event, which appears to separate the first and second pulses of incoming birds. The strongly unimodal peak of pre-sunrise incoming birds, combined with consideration of the time required to visit an inland nest, return to sea, catch a fish and make a second visit, suggested that very few, if any, of the pre-sunrise incoming birds were making repeat entrances. Omitting post-sunrise counts might exclude some murrelets' making first visits, but post-sunrise radar counts were generally low, and such exclusion seems a minor source of error. Manley's (1999) observations at nests within 5 km of the feeding ground, in a similar latitude to Clayoquot Sound, showed that the mean arrival time at nests with chicks was 24 min before sunrise (range 43 min before to 8 min after), while visits to inactive nest sites averaged 22 min before sunrise (range 43 min before to 9 min after), and repeat visits by adults to feed chicks occurred after sunrise.

Effects of Weather.—Fog and misty drizzle are common at dawn in Clayoquot Sound and through much of the murrelet's range. Pre-sunrise counts were often, but not invariably, higher in such weather than on clear mornings. Among cloudy days, there was no significant effect of precipitation, but I could not test the effects of heavy drizzle or rain because this obscured murrelets on the radar screen. Audiovisual detections of murrelets over forests are also usually higher and more prolonged on cloudy or foggy mornings (Rodway et al. 1993*a*, Naslund and O'Donnell 1995). This increase is partly due to increased circling and vocalization of murrelets when visibility is restricted, but my radar data, and those of Cooper et al. (2001) also show that more murrelets are likely to enter forests from the ocean during cloudy weather. High post-sunrise counts, indicating repeated visits, were equally likely on clear, cloudy, or drizzly/foggy mornings.

Seasonal Trends.—The seasonal variations in dawn and dusk counts suggested that dawn counts included all murrelets likely to venture inland, including active breeders, failed breeders, and prospecting nonbreeders, whereas the lower dusk counts included a higher proportion of active breeders. Few murrelets came inland at dusk during incubation (May), but more came in to feed chicks in June and early July. All counts declined and became more variable after mid-July as the breeding season came to an end and murrelets began to leave Clayoquot Sound (personal observations). These variations confirm that evening counts are worth documenting, although lower than dawn counts, because they likely include a higher proportion of active breeders than at dawn and might more accurately show the local breeding chronology.

By restricting sampling to a core period from mid-May through mid-July, seasonal effects were dampened, and I found no significant difference in counts made in the first and second halves of the core period, except for dusk surveys in 1 of the 3 years. This core period covers part of incubation and most of the chick-rearing phase for most murrelets, although the breeding chronology is poorly known for this area (Rodway et al. 1992). The lack of difference between early (mid-May to mid-Jun) and late (mid-Jun to mid-Jul) counts within this core period is puzzling. Early counts should have covered incubation in many pairs, when only 1 of the pair enters the forest at dawn for incubation exchange. During late counts, most pairs should have been raising chicks, and both parents would normally visit the nest each morning (Nelson and Hamer 1995). In addition, young nonbreeders are suspected of entering the forest towards the end of the breeding season (Nelson 1997). Perhaps the numbers of incoming birds in the latter part were offset by those pairs that had failed. Cooper et al. (2001) found strong seasonal variations in incoming radar counts in all 3 years that they sampled.

Annual Variations.—Although considerable variations occurred among years in the counts made at each station, the differences among years were not significant for dawn or dusk counts when all stations were analyzed together. This suggests that similar numbers of murrelets entered the Clayoquot Sound watersheds in each year. The large changes observed among years at some watersheds suggest that movement might occur from 1 watershed to another among years. Because of the high variability among counts at some stations, multiyear surveys are recommended.

Effects of Topography.—Radar is most effective at counting murrelets that are funnelled through narrow inlets or fjords, and is less accurate when the birds go inland across an open coastal plain (Burger 1997). Clayoquot Sound, as well as much of the British Columbia and Alaska coastlines, provides suitable topography for performing radar counts, but much of the southern range is less suitable. Open coastlines could be sampled by surveys made at intervals along the shore, either using a single radar unit moved repeatedly, or preferably, by concurrent surveys with many radar units. Alternatively, radar surveys could be made at inland valleys, although the interference caused by trees and hills often limits the radar's view, especially when murrelets are flying below the tree tops. Avoidance of such interference is 1 advantage of coastline surveys.

If murrelets cross from 1 watershed to another, counts made at the coast might not accurately reflect the numbers using each watershed. Most watersheds sampled in Clayoquot Sound were bordered by mountain ridges hundreds of meters high, and the most convenient flight path for a murrelet would be via the watershed mouth. Some murrelets did, however, cross into adjacent valleys. Murrelets are known to nest at elevations of 1000 m (Jones 1993). In my analysis, I used topographic maps and likely flight lines to assess where murrelets might be crossing from 1 watershed to another and adjusted the inland catchment areas accordingly. More precise estimates of numbers crossing into neighboring watersheds could be attained from radar counts at mountain passes, but the paucity of roads, and the interference from trees and hills, precluded this in Clayoquot Sound.

Habitat Associations and the Effects of Clearcut Logging

Radar counts combined with GIS data allowed an assessment of habitat associations of marbled murrelets at the landscape (watershed) level in Clayoquot Sound, and also provided insights into the effects of clearcut logging on watershed populations. Not unexpectedly, murrelet counts correlated significantly with the size of the watershed and with measures of remaining mature forest, although low-elevation forest below 600 m seemed more important than high-elevation forest. Counts were most strongly correlated with areas of CWHvm1 biogeoclimatic subzone, which made up 96% of the remaining mature forest below 600 m (Matlow). Since Matlow is more easily derived from GIS databases, topographic maps, or timber inventories, it is likely to prove to be a more useful predictor of murrelet populations than the biogeoclimatic subzone.

Multiple regression equations demonstrated the positive effects of low-elevation old-growth and negative effects of logged and immature areas on murrelet counts. Such models are useful for showing the habitat variables apparently affecting counts of murrelets in Clayoquot Sound. They are, however, unlikely to be useful for predicting murrelet numbers in management situations because they require knowledge of the age class, logging history, and biogeoclimatic zones of the area under consideration.

Preliminary analyses of 3 other radar studies found similar relationships between murrelets and available old-growth forest. On northwestern Vancouver Island, north of Clayoquot Sound, Manley (2000) found a significant correlation between Matlow and murrelet numbers. Along the central mainland coast of British Columbia, murrelet counts were significantly correlated with areas of mature forest assessed to be suitable on the basis of forest age, canopy structure, presence of platform limbs, and tree species composition (Schroeder et al. 1999). Raphael et al. (1999) found a positive, but weak association between late-seral habitat and murrelet counts in 9 watersheds on the Olympic Peninsula, Washington, USA.

Radar counts in Clayoquot Sound also revealed impacts of clearcut logging and indicated that when low-elevation old-growth forest is lost, the murrelets did not pack into the remaining forest in higher densities. If they did, counts per watershed would remain constant relative to the areas of original mature forest. In Clayoquot Sound, however, 3 of the 5 watersheds that were extensively logged showed greatly reduced counts. These deviations disappeared when murrelet counts were compared with the remaining low-elevation mature forest, but not when compared with mature forest at all elevations, or with high-elevation mature forest. Evidently, murrelets were responding to loss of low-elevation mature forest by leaving heavily impacted watersheds rather than nesting at higher densities within the remaining habitat. Similar patterns were found by Manley (2000), while Schroeder et al. (1999)

found that murrelet counts at heavily logged watersheds did not show the same relationships with forest area as those in less disturbed watersheds.

Distances from the watershed mouths to the nearest known foraging area varied from 1 to 28 km but had no significant effect on the number of murrelets entering watersheds, even when the effects of habitat had been statistically controlled in multiple regression models. Murrelets are known to fly tens of kilometers from foraging areas to nesting sites (Whitworth et al. 2000).

Use of Radar for Estimating Populations and in Monitoring

This study and other studies (Burger 1997, Cooper and Hamer 2000, Cooper et al. 2001) confirm that radar is the only reliable method for counting murrelets in watersheds. Counts at sea can provide density estimates (Becker et al. 1997) but cannot show where the murrelets might be nesting, and are likely to underestimate murrelet numbers. My counts, which covered most, but not all of the forested areas of the sound and could not account for murrelets missed by the radar, indicate a total regional population in and near Clayoquot Sound considerably larger than the 5,000–6,000 murrelets counted in repeated boat surveys (Sealy and Carter 1984, Kelson et al. 1995).

Although radar has limited application in inland situations due to the interference of trees and hills, radar can also be used inland to count murrelets in smaller, stand-level areas (Hamer et al. 1995). Audiovisual surveys, commonly used to determine the presence and possible nesting-occupancy of murrelets and assess habitat suitability (Rodway et al. 1993*a,b*; Ralph et al. 1995; Evans et al. 2000), cannot provide estimates of actual numbers of birds. No known numerical relationship exists between audiovisual detections and bird numbers (Paton 1995).

In addition to identifying important habitat associations, radar should also be used to monitor the changes in murrelet populations that might occur due to logging, oceanic regime shifts, or other large-scale processes.

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LITERATURE CITED

BECKER, B. H., S. R. BEISSINGER, AND H. R. CARTER. 1997. At-sea density monitoring of marbled murrelets in central California: methodological considerations. Condor 99:743–755.

BURGER, A. E. 1995. Marine distribution, abundance, and habitats of marbled murrelets in British Columbia. Pages 295–312 *in* C. J. Ralph, G. L. Hunt, Jr., M. G. Raphael, and J. F. Piatt, editors. Ecology and conservation of the marbled murrelet. U.S. Forest Service General Technical Report PSW-GTR-152.

———. 1997. Behavior and numbers of marbled murrelets measured with radar. Journal of Field Ornithology 68:208–223.

———. 1999. Radar inventory of marbled murrelets in Clayoquot Sound, 1996–1998. Report to Ministry of Environment, Lands and Parks, Vancouver Island Regional Office, Nanaimo, British Columbia, Canada.

COOPER, B. A., R. H. DAY, R. J. RITCHIE, AND C. L. CRANOR. 1991. An improved marine radar system for studies of bird migration. Journal of Field Ornithology 62:367–377.

———, AND T. E. HAMER. 2000. Appendix H: use of radar for marbled murrelet surveys. Pages 28–34 *in* D. M. Evans, W. P. Ritchie, S. K. Nelson, E. Kuo-Harrison, P. Harrison, and T. E. Hamer, editors. Methods for surveying marbled murrelets in forests: a revised protocol for land management and research. Pacific Seabird Group, Marbled Murrelet Technical Committee, Technical Paper Number 1, revision. Oregon Cooperative Wildlife Research Unit, Oregon State University, Corvallis, USA.

———, M. G. RAPHAEL, AND D. E. MACK. 2001. Radar-based monitoring of marbled murrelets. Condor 103:219–229.

EVANS, D. M., W. P. RITCHIE, S. K. NELSON, E. KUO-HARRISON, P. HARRISON, AND T. E. HAMER, editors. 2000. Methods for surveying marbled murrelets in forests: a revised protocol for land management and research. Pacific Seabird Group, Marbled Murrelet Technical Committee, Technical Paper Number 1, revision. Oregon Cooperative Wildlife Research Unit, Oregon State University, Corvallis, USA.

GREEN, R. N., AND K. KLINKA. 1994. A field guide to site identification and interpretation for the Vancouver Forest Region. Land Management Handbook Number 28. Research Branch, Ministry of Forests, Victoria, British Columbia, Canada.

HAMER, T. E., B. A. COOPER, AND C. J. RALPH. 1995. Use of radar to study the movements of marbled murrelets at inland sites. Northwestern Naturalist 76:73–78.

JODICE, P. G. R., AND M. W. COLLOPY. 2000. Activity patterns of marbled murrelets in Douglas-fir old-growth forests of the Oregon Coast Range. Condor 102:275–285.

JONES, P. H. 1993. Canada's first active marbled murrelet nest discovered and observations. British Columbia Naturalist 31(6):8.

KELSON, J. D., I. A. MANLEY, AND H. R. CARTER. 1995. Decline of the marbled murrelet in Clayoquot Sound, British Columbia: 1982–1993. Northwestern Naturalist 76:90–98.

MANLEY, I. A. 1999. Behavior and habitat selection of marbled murrelets nesting on the Sunshine Coast. Thesis, Simon Fraser University, Burnaby, British Columbia, Canada.

———. 2000. Radar surveys of marbled murrelets on the Northwest Coast of Vancouver Island. Report to Ministry of Environment, Lands and Parks, Vancouver Island Regional Office, Nanaimo, British Columbia, Canada.

NASLUND, N. L., AND B. P. O'DONNELL. 1995. Daily patterns of marbled murrelet activity at inland sites. Pages 129–134 *in* C. J. Ralph, G. L. Hunt, Jr., M. G. Raphael, and J. F. Piatt, editors. Ecology and conservation of the marbled murrelet. U.S. Forest Service General Technical Report PSW-GTR-152.

NELSON, S. K. 1997. Marbled murrelet (*Brachyramphus marmoratus*). The birds of North America, number 276. The American Ornithologists' Union, Washington, D.C., USA, and The Academy of Natural Sciences, Philadelphia, Pennsylvania, USA.

———, AND T. E. HAMER. 1995. Nesting biology and behavior of the marbled murrelet. Pages 57–67 *in* C. J. Ralph, G. L. Hunt, Jr., M. G. Raphael, and J. F. Piatt, editors. Ecology and conservation of the marbled murrelet. U.S. Forest Service General Technical Report PSW-GTR-152.

PATON, P. W. C. 1995. Marbled murrelet inland patterns of activity: defining detections and behavior. Pages 113–116 *in* C. J. Ralph, G. L. Hunt, Jr., M. G. Raphael, and J. F. Piatt, editors. Ecology and conservation of the marbled murrelet. U.S. Forest Service General Technical Report PSW-GTR-152.

RALPH, C. J., G. L. HUNT JR., M. G. RAPHAEL, AND J. F. PIATT. 1995. Overview of the ecology and conservation of the marbled murrelet in North America. Pages 3–22 *in* C. J. Ralph, G. L. Hunt, Jr., M. G. Raphael, and J. F. Piatt, editors. Ecology and conservation of the marbled murrelet. U.S. Forest Service General Technical Report PSW-GTR-152.

RAPHAEL, M. G., D. M. EVANS, AND B. A. COOPER. 1999. Correlating forest habitat distribution with murrelet radar counts: is there a connection at the drainage scale? (Abstract). Pacific Seabirds 26:43.

RODWAY, M. S., H. R. CARTER, S. G. SEALY, AND R. W. CAMPBELL. 1992. Status of marbled murrelets in British Columbia. Pages 17–41 *in* H. R. Carter and M. L. Morrison, editors. Status and conservation of the marbled murrelet in North America. Proceedings of the Western Foundation of Vertebrate Zoology 5.

———, H. M. REGEHR, AND J.-P. L. SAVARD. 1993*a*. Activity patterns of marbled murrelets in old-growth forest in the Queen Charlotte Islands, British Columbia. Condor 95:831–848.

———, ———, AND ———. 1993*b*. Activity levels of marbled murrelets in different inland habitats in the Queen Charlotte Islands, British Columbia. Canadian Journal of Zoology 71:977–984.

SCHROEDER, B. K., M. H. MATHER, AND T. A. CHATWIN. 1999. Reconnaissance inventory of marbled murrelets on the central coast of British Columbia, 1998. Unpublished report, Ministry of Environment, Lands and Parks, Nanaimo, British Columbia, Canada.

SEALY, S. G., AND H. R. CARTER. 1984. At-sea distribution and nesting habitat of the marbled murrelet in British Columbia: problems in the conservation of a solitary nesting seabird. Pages 737–756 *in* J. P. Croxall, P. G. H. Evans, and R. W. Schreiber, editors. Status and conservation of the world's seabirds. Technical Publication Number 2. International Council for Bird Preservation, Norwich, United Kingdom.

WHITWORTH, D. L., S. K. NELSON, S. H. NEWMAN, G. B. VAN VLIET, AND W. P. SMITH. 2000. Foraging distances of radio-marked marbled murrelets from inland areas in southeast Alaska. Condor 102:452–456.

ZAR, J. H. 1996. Biostatistical analysis. Third edition. Prentice-Hall, Upper Saddle River, New Jersey, USA.

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Appendices are on next 2 pages.

Appendix 1. Database of habitat features in 18 watersheds in Clayoquot Sound. See Table 5 for habitat codes.

Watershed	Watershed code	Alpine	Distfeed	Imm	Logged	Logimm	Mature	Maturemm1	Maturevh1	Maturevm1	Maturevm2	Mathigh	Matlow	Origforest	Totarea
Atleo	AT	0	8	0	949	949	1,762	96	255	900	511	607	1,155	2,711	2,732
Bedwell (excluding Ursus)	BE	2,710	22	1,603	456	2,059	8,577	2,593	0	2,942	2,947	5,540	2,942	10,540	13,598
Boat Basin	BB	0	8	0	379	379	5,250	0	232	4,342	675	**675**	**4,574**	**5,628**	**5,672**
Bulson	BU	705	18	0	167	167	7,981	1,064	197	3,466	3,247	4,311	3,662	8,140	8,856
Clayoquot + 0.5 upper Kennedy	CR	983	22	0	60	60	8,329	440	0	4,663	3,225	3,665	4,663	8,388	9,432
Cypre	CY	125	7	0	2,115	2,115	3,523	364	342	1,427	1,390	1,754	1,769	5,638	5,763
Flores Creek #6	F6	0	2	0	0	0	1,742	0	275	1,389	78	78	1,664	1,742	1,742
Hesquiat Point	HP	0	1	0	15	15	1,752	0	55	1,514	182	182	1,570	1,767	1,767
Kennedy (excluding upper valley)	KE	2,094	20	646	2,154	2,800	13,842	1,555	0	6,565	5,700	7,255	6,565	16,620	18,769
Megin (West Megin only)	ME	398	15	0	0	0	10,321	502	0	8,189	1,630	2,132	8,189	10,321	10,745
Moyeha	MO	4,393	16	0	0	0	12,935	2,826	0	5,365	4,559	7,385	5,365	12,750	17,930
Pretty Girl	PG	167	15	0	0	0	3,362	72	0	2,706	584	656	2,706	3,362	3,540
Sydney	SY	47	18	0	0	0	5,517	126	0	3,985	1,406	1,532	3,985	5,517	5,591
Tofino Creek + 0.5 upper Kennedy	TC	750	28	0	383	383	5,232	490	2	2,623	2,117	2,607	2,624	5,615	6,454
Tranquil	TR	439	22	0	1,056	1,056	4,358	622	0	1,977	1,759	2,381	1,977	5,414	5,870
Ursus	UR	919	24	44	0	44	6,367	1,251	0	3,032	2,082	3,333	3,032	6,409	7,348
Watta (includes East Megin)	WA	2,334	18	0	0	0	14,951	2,117	13	7,857	4,964	7,081	7,870	14,951	17,341
Watta South	WS	0	16	0	0	0	1,394	212	22	667	493	705	689	1,394	1,394

Appendix 2. Pearson correlations among habitat variables in 18 watersheds in Clayoquot Sound. See Table 5 for habitat codes.

	Alpine	Distfeed	Imm	Logged	Logimm	Mature	Maturemm1	Maturevh1	Maturevm1	Maturevm2	Mathigh	Matlow	Origforest
Distfeed	0.389	1.000											
Imm	0.446	0.265	1.000										
Logged	0.003	–0.039	0.240	1.000									
Logimm	0.203	0.089	0.640**	0.899**	1.000								
Mature	0.788**	0.460	0.277	0.058	0.170	1.000							
Maturemm1	0.953**	0.446	0.548*	0.026	0.267	0.780**	1.000						
Maturevh1	–0.412	–0.685**	–0.218	0.342	0.173	–0.435	–0.384	1.000					
Maturevm1	0.499*	0.310	0.064	–0.087	–0.040	0.893**	0.470*	–0.415	1.000				
Maturevm2	0.814**	0.551*	0.323	0.226	0.325	0.927**	0.808**	–0.401	0.687**	1.000			
Mathigh	0.895**	0.527*	0.401	0.147	0.297	0.922**	0.912**	–0.410	0.653**	0.975**	1.000		
Matlow	0.481*	0.283	0.063	–0.060	–0.019	0.870**	0.446	–0.372	0.996**	0.670**	0.628**	1.000	
Origforest	0.782**	0.454	0.385	0.233	0.358	0.981**	0.788**	–0.378	0.841**	0.942**	0.931**	0.833**	1.000
Totarea	0.873**	0.454	0.416	0.182	0.332	0.974**	0.864**	–0.401	0.790**	0.947**	0.960**	0.780**	0.986**

* $P < 0.05$
** $P < 0.01$