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Breeding chronology of Marbled Murrelets varies between coastal and inshore sites in southern British Columbia

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ABSTRACT. We used four methods to compare the breeding chronologies of Marbled Murrelet at two sites at similar latitudes in British Columbia: Desolation Sound on the mainland, inshore of the Strait of Georgia, and Clayoquot Sound on the west coast of Vancouver Island. At both sites, we estimated breeding chronologies from the timing of (1) nest initiation dates determined by radio-telemetry, (2) the chick feeding period determined from observations of fish-holding adults, (3) hatch dates determined from observations of juveniles on the water, and (4) brood patch scores determined from captured birds. At Desolation Sound, these methods each produced a similar distribution of nesting dates, but at Clayoquot Sound, the distribution of nesting dates of radio-tracked birds were substantially biased towards later nests. Despite these methodological difficulties, we found that Marbled Murrelets at Desolation Sound bred ca. 30 d later than at Clayoquot Sound. Regional differences in breeding chronology of this magnitude, if not properly calibrated, would bias estimates of peak inland activity, and should be considered in forestry operations, the interpretation of census data, and the design of monitoring programs.

SINOPSIS. Cronología reproductiva variable de *Brachyramphus marmoratus* en localidades cerca de la costa y tierra adentro en la British Columbia

Utilizamos cuatro métodos para comparar la cronología reproductiva de *Brachyramphus marmoratus* en dos localidades de similar latitud en la Columbia Británica. Estos fueron: Desolation Sound en tierra firme, en la parte interna del Estrecho de Georgia, y Clayoquot Sound en la costa oeste de la isla de Vancouver. En ambas localidades, estimamos la cronología reproductiva desde 1) fecha de iniciación de anidar determinada por radioteleletría, 2) el periodo de alimentación de los polluelos, determinado visualmente (adultos cargando peces), 3) fecha de eclosionamiento (abandono del nido) determinada mediante observación de polluelos en el agua y 4) presencia del parcho de incubación, determinado en aves capturadas. En Desolation Sound, los métodos mencionados produjeron una distribución similar de fechas en lo referente al comienzo de nidos, pero en Clayoquot, la distribución de fechas de anidamiento tuvo sesgo hacia el final de la temporada reproductiva. No empecé a dificultades con la metodología, encontramos que las aves de Desolation se reprodujeron 30 días ms tarde que las de Clayoquot. Si no se calibran adecuadamente, diferencias regionales de esta magnitud, (en la cronología reproductiva de la especie), se obtendrá sesgo en el estimado del pico de la actividad reproductiva en tierra adentro. Esto se debe tomar en consideración en las operaciones forestales, la interpretación de censos y en el diseño de programas de monitoreo.

Key words: Clayoquot Sound, Desolation Sound, Marbled Murrelet, nesting timing, radio telemetry

Knowledge of the breeding chronology of Marbled Murrelets (*Brachyramphus marmoratus*) is critical to accurately evaluating local activity patterns and habitat use (Hamer and Nelson 1995) and to estimating murrelet productivity based on juvenile ratios derived from at-sea census data (Kuletz and Kendall 1998). In addition, understanding variation in dates and du-

ration of inland nesting activity across the murrelets' range will provide researchers and managers with better information for the scheduling of potential forestry activity (Hamer and Nelson 1995).

At a broad scale, Marbled Murrelets breed later at higher latitudes (Hamer and Nelson 1995). However, there has been little examination of variation in murrelet breeding chronology at a regional scale, when latitude varies little. In this case, the breeding ecology of seabirds is expected to vary when local populations occupy different marine environments, likely due to differences in food supply (Wilson and Manuwal 1986). We studied Marbled Murre-

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lets at two marine sites in British Columbia: Desolation Sound inland of the Strait of Georgia, sheltered from the Pacific Ocean by Vancouver Island, and Clayoquot Sound on the west coast of Vancouver Island, exposed to the open Pacific Ocean.

The breeding chronology of Marbled Murrelets has been notoriously difficult to study because of their cryptic and solitary nesting behavior (Nelson 1997; Cooke 1999). In addition, breeding by Marbled Murrelets is highly asynchronous (Hamer and Nelson 1995; Loughheed et al. 2002a; Tranquilla et al. 2003a), causing breeding stages (e.g., pre-breeding, egg-laying, incubation, chick-rearing, fledging) to overlap considerably within populations. The asynchronous breeding season likely reflects both differences in the timing of initial breeding attempts (Loughheed et al. 2002a; Tranquilla et al. 2003a), and replacement laying following nest failure (Hebert et al. 2003; Tranquilla et al. 2003b; Nelson and Hamer 1995). Our primary objective was to estimate and compare the timing of egg-laying at our two sites, using four methods, building on a previous study at Desolation Sound (Loughheed et al. 2002a). We did this by using (1) radio telemetry to document egg-laying and the onset of incubation at individual nests (Bradley et al. 2004); (2) the presence of fish-holding adults to document chick-rearing periods; (3) the timing of appearance of juveniles on the water to document fledging periods (Hamer and Nelson 1995; Loughheed et al. 2002a); and (4) a measure of brood patch development of captured birds (Tranquilla et al. 2003c). Our secondary objective was to assess potential biases associated with each technique used to estimate timing of breeding.

METHODS

Study sites and seasons. Desolation Sound (centre 50°05'N, 124°40'W) is an inlet off the Strait of Georgia, on the mainland coast of British Columbia. Clayoquot Sound (centre 49°12'N, 126°06'W) is on the outer coast of Vancouver Island, British Columbia. The sites are 142 km apart. Compared to Clayoquot Sound, Desolation Sound is more sheltered from both maritime weather and Pacific currents (i.e., the Subarctic and California currents) and warms up more over the course of

the summer. Fieldwork was conducted in Desolation Sound, with a primary goal of capturing Marbled Murrelets for radio-tracking and locating nests (Bradley et al. 2004), from May to August 1998, April to September 1999, and April to August 2000 and 2001. Fieldwork with a similar goal was conducted in Clayoquot Sound from May to June 2000, late April to June 2001, and late April to July 2002. Field crews encountered and captured birds daily, weather permitting, within these time periods.

Estimating temporal distributions of breeding stages. We estimated nesting dates from the behavior patterns of radio-tracked birds (Bradley et al. 2002, 2004; Loughheed et al. 2002a). Birds were captured by field crews in inflatable boats (Zodiacs), using spotlights to locate birds at night (ca. 22:00 to 05:00 PST) and scoop them from the surface of the water with long-handled fishnets (Whitworth et al. 1997). Radio transmitters (transmitter model 386, Advanced Telemetry Systems, Isanti, MN) were attached to individual birds with subcutaneous anchors (Newman et al. 1999; Loughheed et al. 2002b) and epoxy (Bird Adhesive, Titan Corporation, USA) in 1999–2000 or Verbond[®] tissue adhesive (3M Animal Care Products, USA) in 2001 and 2002. Lifetime of the transmitters was at least 80 d. Radio-tagged birds were located daily by helicopter subsequent to radio attachment, until the end of the field season or until the radio transmitter signals disappeared. Both sexes of Marbled Murrelets incubate the egg for 24-h shifts (Simons 1980). We estimated the onset of incubation to have occurred when radio-tagged murrelets began a distinct pattern of incubation shifts (inland one day on the nest, and at sea every second day; Bradley et al. 2004). Because Marbled Murrelets have a clutch size of one, the day on which this attendance pattern began was considered to be the nesting date. We use the term “nesting date” to indicate the day on which the egg was laid and incubation began.

We estimated the timing of the chick-rearing period by tallying all fish-holding adult murrelets (hereafter called “fish-holders”) captured or encountered on each date sampled. Marbled Murrelets typically capture a single fish to feed their young during the night, hold it in their beaks while waiting on the water, and deliver it to the nest just prior to dawn (Sealy 1974). No fish-holders included in this study were recap-

tured within the same year, so we treat each sighting as independent and our counts as representing total numbers of individual birds.

We estimated a chick fledging distribution based on juveniles observed or captured at sea at night on each date sampled. Juvenile murrelets were recognized by plumage (Carter and Stein 1995; Kuletz and Kendall 1998) and additionally, when captured, by their mass and the presence of egg teeth. Because we were able to get very close to the birds while dip-netting and each bird was brightly illuminated in the spotlight, juvenile and adult plumages were readily distinguished from each other.

Many adult murrelets captured at sea were neither fish-holding nor radio-tagged, yet were likely breeding birds. To provide a general measure of the potential breeding timing at each site using a larger sample size, we compared the developmental stages of brood patches of dip-netted birds, scored following Sealy (1972; Tranquilla et al. 2003c). We compared the seasonal distributions of the proportion of birds with fully developed (vascularized and edematose) brood patches in 10-d intervals.

We explored potential temporal biases among our methods as measures of breeding chronology within sites by examining their internal consistency against our expectations based on the timing of murrelet breeding stages outlined by Nelson and Hamer (1995). We did not include the brood patch distribution in these comparisons because the temporal relationships between full brood patch development and laying dates are too variable to allow us to establish a predicted relationship (Tranquilla et al. 2003c).

The distribution of nesting dates from radio-tracked birds was used directly. To provide a simple picture of potential temporal biases in the radio samples at each site, we calculated "relative nesting dates" within each site by subtracting each radio date from the earliest nesting record for each site in each year, as backdated from fish-holders or juveniles (see below). The earliest backdated date always preceded the earliest radio date.

We backdated our chick-rearing period to produce potential nesting dates by subtracting the average duration of incubation, ca. 30 d (Nelson and Hamer 1995), from each observation made of fish-holders. Because fish-holding occurs throughout the 28-d chick-rearing

period, as opposed to the single-day event of laying the egg, we expect the egg-laying distribution backdated from fish-holders to be later than the actual nesting event. Thus, we expect the median of our nesting distribution to fall ca. 14 d later than the true distribution of egg-laying. Failure during rearing would skew the distribution towards earlier observations, because fish-holding would drop out for some pairs.

We backdated our juvenile distribution to produce potential nesting dates by subtracting the average duration of incubation plus that of chick-rearing, ca. 58 d (Nelson and Hamer 1995), from each observation made of juveniles. Again, we expected to find a later distribution relative to true egg-laying, because juveniles were unlikely to be encountered on the first day after fledging. However, juvenile residency time, at least in Desolation Sound, is short (5.4 d; Loughheed et al. 2002b; N. R. Parker et al., unpubl. data); thus, we expected to find this distribution intermediate between the sample of true dates (e.g., those derived from an unbiased sample of radio-tagged individuals) and those estimated from fish-holders.

Our fieldwork in Desolation Sound extended over most of the chick-rearing and juvenile periods. However, at Clayoquot Sound, our field season primarily overlapped with nesting and chick rearing periods, but the post-fledging sampling period was shorter, resulting in a truncated distribution of juveniles toward the end of each season. For this reason, we have excluded the nesting dates estimated from juveniles from our overall estimation of site differences in breeding chronology (see below).

Data analysis. We compared the distribution of nesting dates using general linear models and ANOVA with Tukey's means comparisons (JMP 1989–2002). Models were fitted with nesting dates as the response variable and site, methods, year, and all biologically relevant interactions, as explanatory variables. All models were examined for deviations from normality using normal probability and residual plots. Chi-square tests were used to compare the proportion of nesting murrelets at each site. Means \pm 1 SE are reported, except where otherwise indicated.

RESULTS

Methodological variation in nest date estimates. At Desolation Sound, 290 radio-

tagged birds (1998–2001) were tracked, of which 121 (41.7%) were determined to be incubating. We observed 55 fish-holding adults and 145 juveniles. The brood patches of 779 murrelets were assessed, of which 403 had fully developed brood patches. At Clayoquot Sound, 210 radio-tagged birds (2000–2002) were tracked, of which 34 (16.2%) were determined to be incubating. We observed 41 fish-holding adults and 73 juveniles. The brood patches of 231 murrelets were assessed, of which 123 had fully developed brood patches.

At Desolation Sound, the relative temporal distributions of nesting dates from radio-tagged birds, fish-holders, and juveniles overlapped approximately as expected (Fig. 1A). However, we found a small but significant variation between timing of nesting determined by each method (Table 1, Fig. 1A); mean nesting date backdated from fish-holding adults ($4 \text{ June} \pm 2$) was ~ 8 d later than that estimated from radio-tagged birds ($27 \text{ May} \pm 1.4$) and the appearance of juveniles at sea ($27 \text{ May} \pm 1.3$, Fig. 1A).

In contrast, at Clayoquot Sound, relative temporal distributions of nesting dates from the three methods were substantially different (Table 1, Fig. 1B). Mean nesting date estimated from radio-tagged birds ($2 \text{ June} \pm 2.0$) was a month later than those backdated from fish-holders ($4 \text{ May} \pm 1.8$) and juveniles ($2 \text{ May} \pm 1.6$, Fig. 1B).

Annual variation. At Desolation Sound, nesting date estimated from the three methods pooled varied significantly with year (GLM; Table 1, Fig. 2) Nesting occurred ca. 10 d earlier in 2001 than in 1998–2000. Although estimated nesting dates varied between years, we detected no annual variation in the occurrence of fully developed brood patches (ANOVA, $F_{3,399} = 0.24$, $P = 0.87$) at Desolation Sound.

Similarly, in Clayoquot Sound, estimated nesting date was predicted to start ca. 5 d earlier in 2001 than in other years (GLM; Table 1, Fig. 2). Although there is a significant year*method interaction, this difference is largely due to the truncation of sampling for juveniles in the first two seasons. We see the same pattern in nesting date if we analyze annual variation using only fish-holders (ANOVA, $F_{2,38} = 3.12$, $P = 0.06$, Fig. 1B). The occurrence of fully-developed brood patches did not vary significantly by year (ANOVA, $F_{2,120} = 2.61$, $P = 0.08$).

Site variation. The large discrepancy between estimated nesting dates from radio telemetry and the other two methods at Clayoquot Sound suggests that the radio-tagged sample is biased towards later-nesting individuals at this site. To further evaluate this, we examined the relationship between the timing of breeding by the radio-tagged sample and relative nesting date at both sites. At Desolation Sound, radio-tagged birds were captured earlier relative to the start of the breeding season (i.e., calculated from the earliest backdated nesting date at each site) than those at Clayoquot Sound ($F_{1,155} = 69.5$, $P < 0.0001$; Fig. 3). In addition, a higher proportion of murrelets were captured prior to incubation in Desolation Sound (93.4%, $N = 121$) than Clayoquot Sound (82%, $N = 34$; $\chi^2 = 3.85$, $P = 0.05$).

To remove the confounding influence of estimation method, we calculated inter-site differences in nesting date using only fish-holding birds. Nesting dates from radio telemetry were excluded because they included relatively late breeders in Clayoquot Sound. We also excluded juveniles because the short duration of fieldwork in Clayoquot Sound in 2000 and 2001 biased our observations toward earlier nesting birds. Using dates from fish-holders only, the timing of breeding in Desolation Sound was 30 d later than at Clayoquot Sound (ANOVA, $N = 96$, $F_{1,94} = 81.5$, $P < 0.01$). This was also the case when the analysis was restricted to 2000 and 2001, when field sites were monitored concurrently (ANOVA, $N = 54$, $F_{1,52} = 41.6$, $P < 0.001$).

The seasonal distribution of fully developed brood patches differed between Desolation and Clayoquot Sounds, with modes approximately two weeks apart ($N = 424$, $\chi^2 = 3.93$, $P = 0.05$; Fig. 4).

DISCUSSION

Our study produced two main results: that radio tracking Marbled Murrelets to nest sites produced a biased nesting chronology, particularly at Clayoquot Sound; and that Marbled Murrelets start nesting approximately one month later in Desolation Sound than in Clayoquot Sound.

Methodological variation. Although we predicted slight variation between the nesting dates from radio-tracking, chick-rearing, and

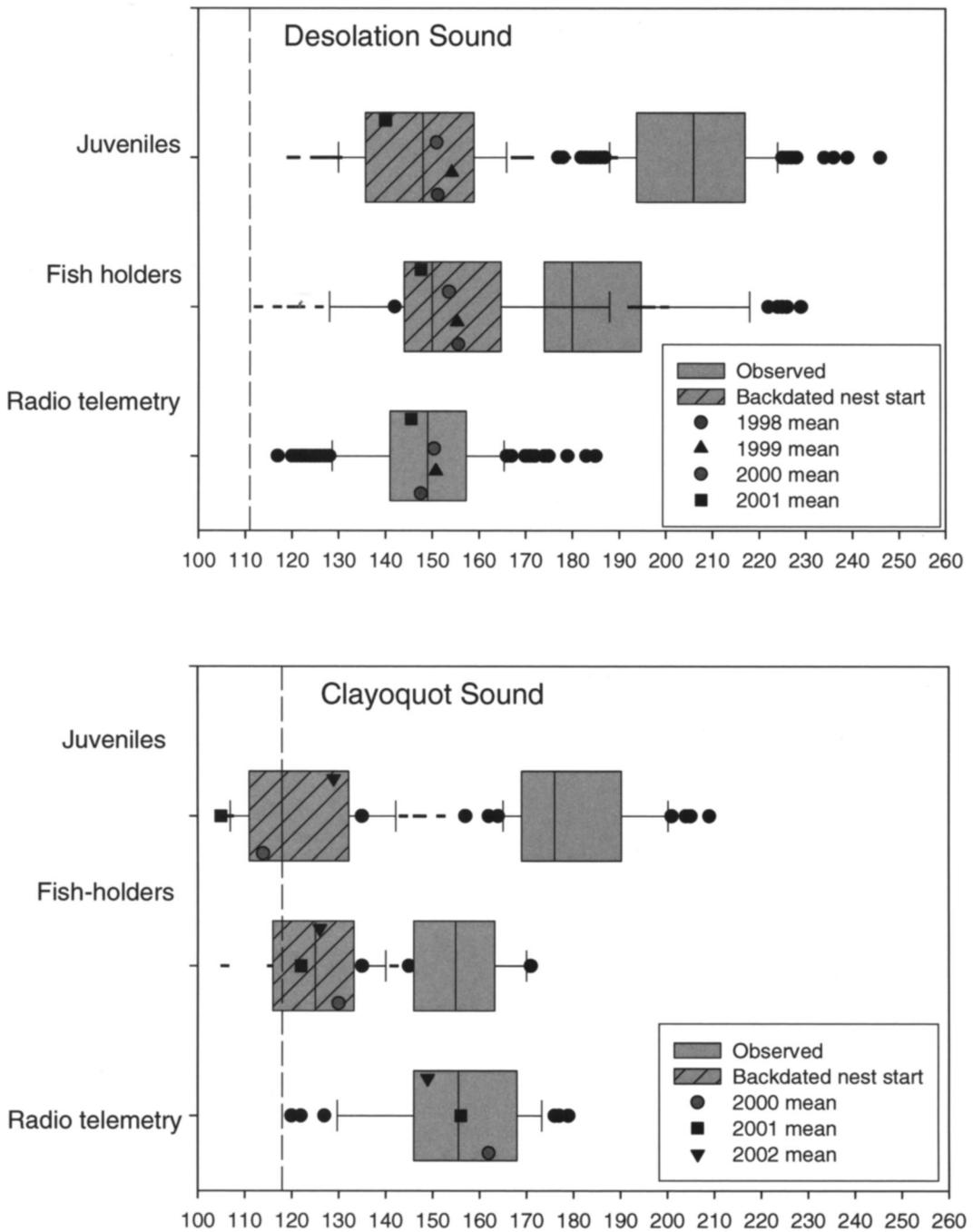


Fig. 1. Nesting start dates (from radio telemetry) of Marbled Murrelets, and observations of at-sea fish holders and juveniles, with corresponding back-dated nesting dates, in Desolation Sound and Clayoquot Sound, B.C. Box plots show quartiles, dotted lines in boxes show means, solid lines show medians, and whiskers indicate the 10th and 90th percentiles. Outliers are shown as filled circles for observed data and as dashes for backdated distributions. Dashed vertical lines indicate starting date of capture effort. Julian date 100 = 10 March.

Table 1. General linear model examining the effects of inter-annual and methodological variation on the timing of Marbled Murrelet nesting at Clayoquot Sound (2000–2002) and Desolation Sound (1998–2001).

Site	<i>N</i>	df	<i>F</i>	<i>P</i>
Desolation Sound				
Overall	341	11, 330	5.32	<0.0001
Year	341	3	4.30	0.005
Method	341	2	5.96	0.003
Year*method	341	6	1.49	0.18
Clayoquot Sound				
Overall	145	2, 137	31.92	<0.0001
Year	145	2	3.50	0.03
Method	145	2	118.4	<0.001
Year*method	145	4	9.91	<0.001

juvenile distributions at Desolation Sound, all produced similar estimates (Fig. 1A). The mean nesting date from fish-holders was later than that observed using radio telemetry, but not by as much as we predicted (8 vs. 14 d). Likewise, the mean nesting date from the juvenile distribution was the same as the radio nesting date, instead of later. These relationships suggest that even at Desolation Sound, we missed radio-tagging the earliest nesting birds. This is supported by our slightly right-skewed distribution of nesting murrelets relative to the start of the season at Desolation (relative nesting dates; Fig. 3).

At Clayoquot Sound, we found a large discrepancy between backdated nesting dates and those observed by radio telemetry. Backdated nesting dates from fish-holding and juvenile periods were only 2 d apart (Fig. 1B), when we expected approximately an 8-d difference. If radio-tagging had sampled nesters throughout the breeding season, our mean nesting dates backdated from fish-holders and juveniles should have been later than that estimated from the radio-tagged birds, due to the longer duration of the chick-rearing and juvenile periods, compared to the nesting date. Instead, mean backdated nesting dates were much earlier than those observed by radio telemetry. Similarly, the distribution of nesting relative to the start of the season (Fig. 3) was right-skewed, with radio-tagged murrelets nesting later in the season than might be expected. Together, these suggest that our telemetry sample at this site captured

only late nesters. Indeed, if we had estimated egg-laying on telemetry alone, we would have estimated that egg-laying in Clayoquot occurred later than at Desolation Sound.

The relative accuracy of radio telemetry in estimating nesting dates appears to be related to differences in murrelet behavior between Clayoquot and Desolation Sounds. Adult Marbled Murrelets at Desolation Sound were inshore throughout the study period (L. M. Tranquilla, pers. obs.), allowing for capture prior to incubation. In contrast, adult murrelets in Clayoquot Sound appeared to fly offshore at night early in the season (N. R. Parker, pers. obs.), moving into the inlets at night later in the season. This pattern of movement is consistent with a previous radar study in Clayoquot Sound, when fewer murrelets came inland during May, and more murrelets came into the inlets in June and early July (Burger 2001). Because of these behavioral differences between sites, the timing of radio tagging in Clayoquot Sound resulted in fewer captures prior to incubation (82% in Clayoquot vs. 91% in Desolation) and a smaller proportion of nesters amongst the radio-tagged birds (22.6% in Clayoquot vs. 41.7% in Desolation). Thus, radio telemetry alone was insufficient to compile a breeding chronology in Clayoquot Sound, not because of the radio telemetry methods *per se*, but because of the murrelets' nighttime accessibility early in the season.

In turn, this difference in nighttime murrelet behavior at the two study sites may be related to seasonal shifts in the distribution of prey, or changes in the energetic requirements of adults or young with breeding stage, causing variation in movement and foraging patterns (Ashmole 1971; Montevecchi 1993). For example, penguins change their foraging patterns, both in response to changes in prey abundance near the colony and the energetic requirements of chicks (Charrassin et al. 1998; Forero et al. 2002). Marbled Murrelets in California were able to change their foraging strategies to exploit limited and changing prey resources and distribution (Becker and Beissinger 2003). However, murrelets are known to forage in straits, not offshore (Hay 1992; Mahon et al. 1992) and not at night (Jodice and Collopy 1999). Thus, we are not sure what the Clayoquot Sound murrelets were doing offshore early in the breeding season. In Desolation Sound, the distribution

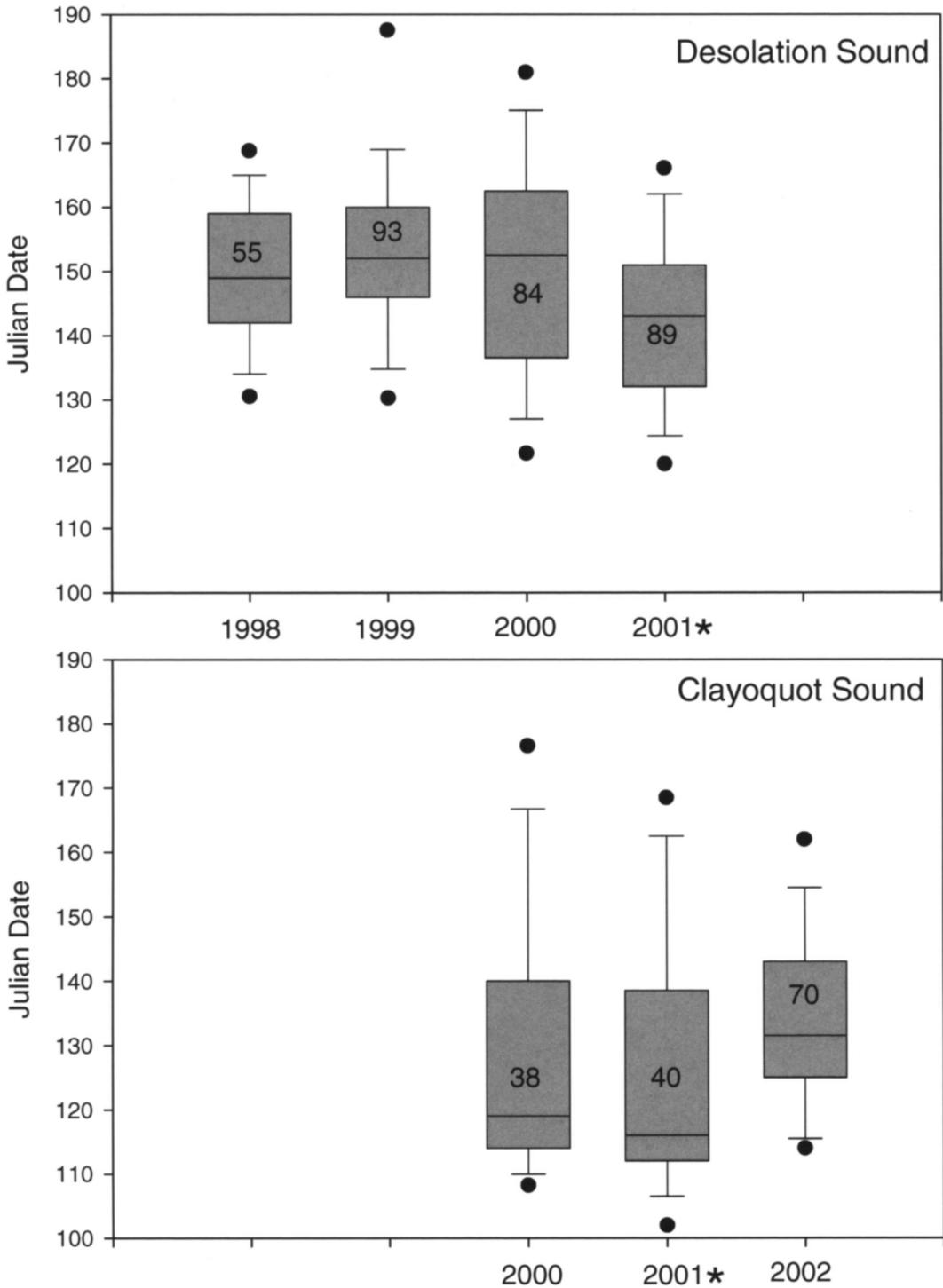


Fig. 2. Annual variation in nest start dates, including both backdated and observed data in Desolation Sound and Clayoquot Sound, B.C. At both sites, 2001 was significantly different from other years (GLM; Table 1). Boxplot details are as in Figure 1. Sample sizes are indicated inside boxes.

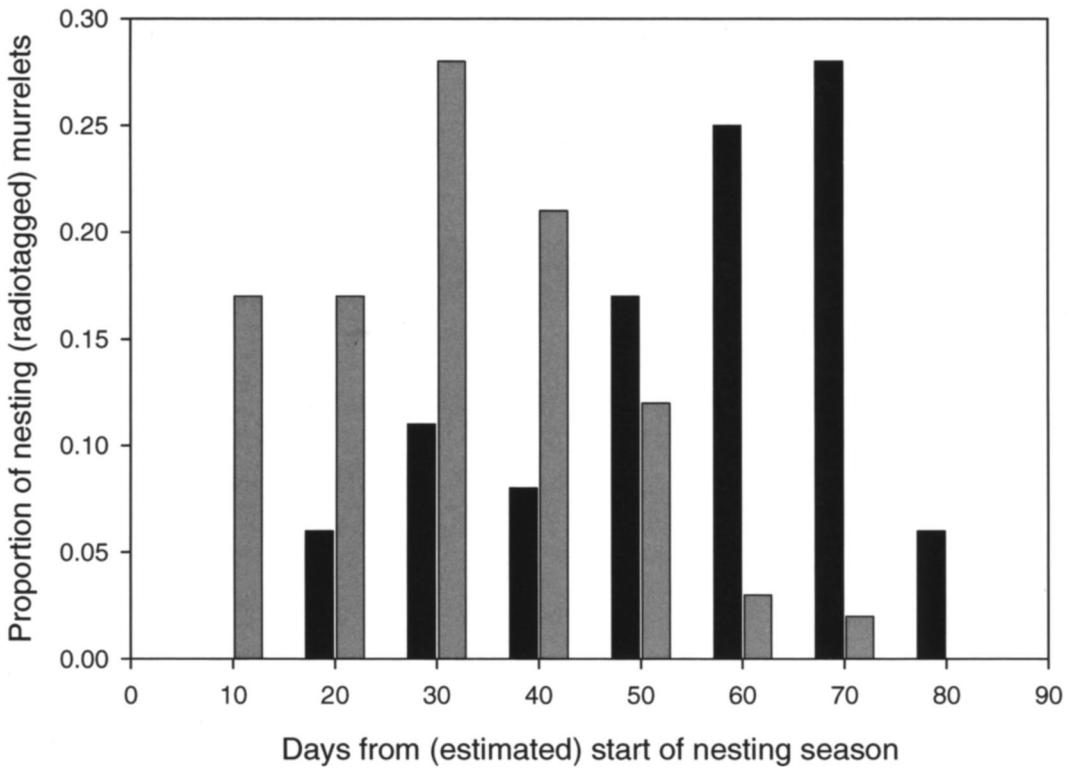


Fig. 3. More radio-tagged birds nested early in the season in Desolation Sound than in Clayoquot Sound (where day 0 was relative start of nesting season). Vertical axis shows proportion of nesting, radio-tagged murrelets; horizontal axis shows days from estimated start of nesting season at each site. Dark bars represent Clayoquot Sound and light bars Desolation Sound.

of murrelets between day and night did not seem to change. Radio-tracking of murrelets in Desolation Sound throughout the breeding seasons did not reveal nighttime offshore movements; ca. 290 radio-tracked murrelets at this site stayed in the inlet and in the Strait of Georgia, and did not ever travel across Vancouver Island to the Pacific Ocean proper.

Site variation. Despite the discrepancy in the radio-tagging data, we found that nesting starts about 1 mo earlier in Desolation than in Clayoquot Sound. This finding was consistent among three of the four methodologies we used to compare inter-site nesting (Fig. 1). Although a strong relationship exists between latitude and the timing of the breeding season among Marbled Murrelets from California to Alaska (Nelson and Hamer 1995), this is unlikely to explain the differences in breeding chronology between our two sites, as they are only separated by one degree of latitude. In this case, it is more

likely that variation in seabird breeding chronology was related to large-scale weather processes, oceanic conditions, and prey availability (Ainley and Boekelheide 1990; Gaston and Smith 2001; Gjerdrum et al. 2003; Hodum 2002; Loughheed et al. 2002a; Ramos et al. 2002). Likewise, oceanic influences (wind, tides, and currents) affecting food availability are expected to be different at offshore versus inshore sites (Wilson and Manuwal 1986; Abookire et al. 2000; Robards et al. 2002). Because Clayoquot Sound is directly adjacent to the Pacific Ocean, and Desolation Sound is sheltered from the ocean by Vancouver Island, it is likely that our study has captured site variation in breeding timing caused by differences in oceanic and foraging conditions. For instance, Wilson and Manuwal (1986) found a difference between prey species brought to nestlings on coastal versus inshore colonies of Rhinoceros Auklets (*Cerorhinca monocerata*) in

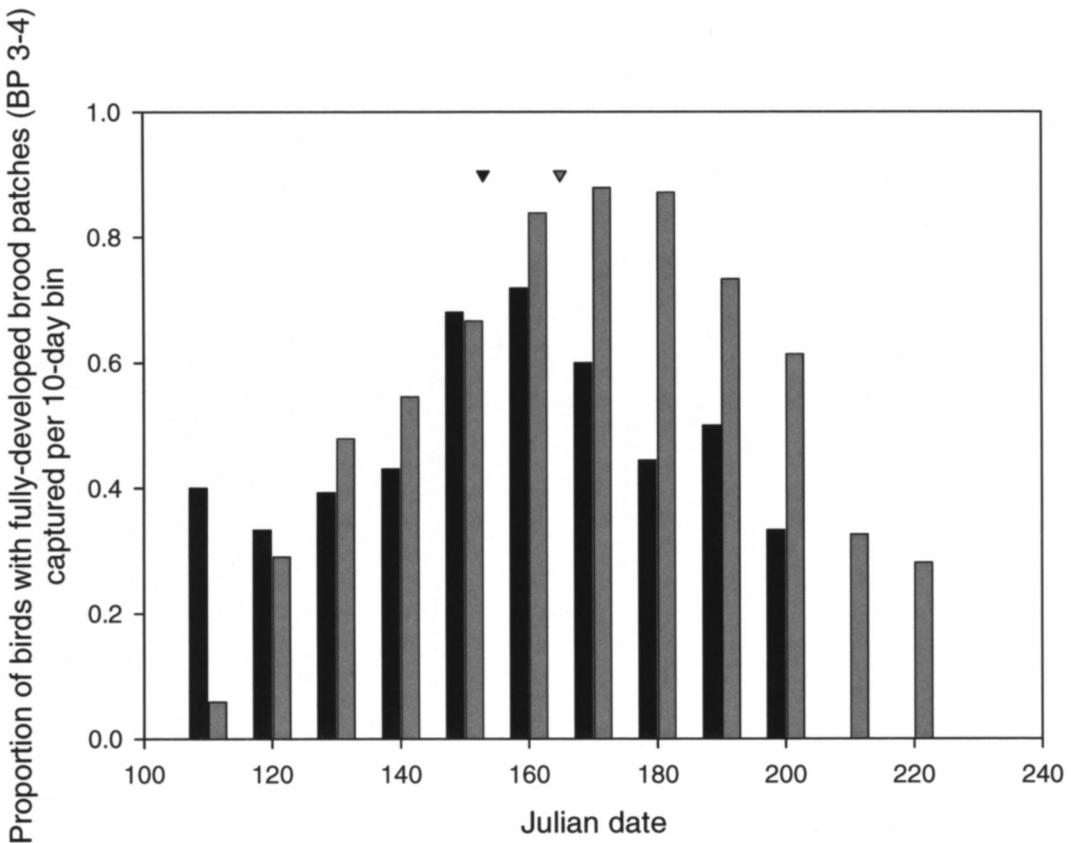


Fig. 4. Histogram showing percent frequency and mean dates of birds with fully developed brood patches captured per 10-d period at Desolation Sound ($N = 779$) and Clayoquot Sound ($N = 231$). Dark bars represent Clayoquot Sound and light bars Desolation Sound. Julian date 100 = 10 March.

Washington. Unfortunately there is little detailed information about the abundance, distribution, or movements of Marbled Murrelet forage fishes at Clayoquot or Desolation Sounds.

In addition to oceanic conditions, Marbled Murrelet breeding is likely to be influenced by regional terrestrial microclimate. Marbled Murrelets are unique in nesting in old growth forests (Nelson 1997), often at very high elevations on mountain ranges (Zharikov et al. 2005). Most nests we have found at Desolation Sound (mean elevation, 700 ± 345 m) are at higher elevation than those at Clayoquot Sound (565 ± 334 m). In addition, snowpack at mountain ranges on Vancouver Island is typically less than that on the mainland coast (Snow survey data; www.wlap.gov.bc.ca/rfc/river_forecast). If snowpack influences timing of breeding in murrelets, we might expect Desolation Sound nest-

ing to occur later than at Clayoquot, due to later snow melt at that site. However, we know anecdotally that murrelets do initiate nesting when snowpack is still high in Desolation Sound.

We recommend that when using radio telemetry, other methods should be used to help mitigate methodological bias and corroborate results. If time and resources are limited, we suggest that inter-site variation in breeding chronology could be assessed by concentrating marine surveys during the fish-holding (i.e., chick-rearing) period. Because inter-site variation in breeding chronology has management implications for population monitoring and conservation of Marbled Murrelets, it is particularly important to better understand how murrelet breeding chronology is influenced by periodic environmental phenomena. Regional

differences in breeding chronology of the magnitude found in our study, if not properly calibrated, would bias estimates of peak inland activity used to determine when to conduct radar studies or forest activity surveys. Modification or temporal restriction of forest industry activities during the Marbled Murrelets' breeding season will require specific knowledge of how regional breeding chronology varies along the coast of British Columbia.

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