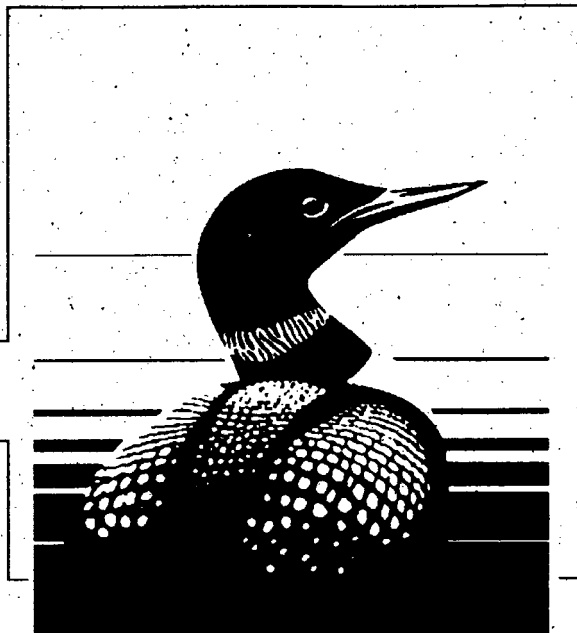

Breeding Chronology, Breeding Success, Distribution and Movements of Marbled Murrelets (*Brachyramphus marmoratus*) in Desolation Sound, British Columbia

Cecilia Lougheed

Pacific and Yukon Region 2000
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**BREEDING CHRONOLOGY, BREEDING SUCCESS, DISTRIBUTION AND
MOVEMENTS OF MARBLED MURRELETS (*Brachyramphus marmoratus*)
IN DESOLATION SOUND, BRITISH COLUMBIA**

Cecilia Lougheed

This report is a verbatim copy of the M.Sc. research which Cecilia Lougheed carried out in partial fulfilment of the requirements for the Degree of Master of Science at Simon Fraser University. It is reproduced as a CWS Technical Report here in order to allow a wide circulation to a broader readership.

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ABSTRACT

The breeding chronology, breeding success, distribution and movements of a Marbled Murrelet (*Brachyramphus marmoratus*) population were studied at Desolation Sound, British Columbia from 1996 to 1998. This threatened seabird (family Alcidae) spends most of its time at sea and feeds on small fish, but is unique among the auks for nesting solitarily in old-growth forest. I integrated several methods to study the chronology and synchrony of breeding by this population. I used radio telemetry to study local survival (and emigration rates) of hatch year (HY) and after-hatch year (AHY) birds. I also used at-sea surveys and radio telemetry to study fine scale changes in spatial and temporal distribution of birds on the ocean.

The timing of breeding events varied among years (1996 was earliest, 1998 was the latest). The breeding seasons were long and had a large overlap between incubation and chick rearing. An average breeding season extended from April 21 to September 5. Marbled Murrelets in Desolation Sound breed more asynchronously than predicted for an alcid at this latitude.

I calculated juvenile ratios (the ratio of HY to AHY birds) with two methods: (1) using HY numbers corrected for emigration rate and the mean AHY number during the peak counts of the season (the “corrected” ratio); and (2) using counts of HY and AHY birds from the same late season surveys (the “concurrent” ratio). The weekly survival rate of newly radio-tagged HY birds was 0.27 (0.73 emigration rate); it was 0.95 for AHY birds (0.05 emigration rate). The average “corrected” juvenile ratio was higher (0.131 ± 0.053) than the “concurrent” juvenile ratio (0.042 ± 0.022) but lower than other independent estimates of fecundity from nest site monitoring. I propose that my juvenile ratio estimates are lower due to differences in at-sea distribution of adults and juveniles. I emphasize that these estimates must be cautiously interpreted, due to the unknown extent of the bias in AHY numbers.

Marbled Murrelets in Desolation Sound undertake both daily and seasonal movements related to breeding. They are usually denser in areas of cooler water, but shift their distribution towards areas close to the old-growth forest, especially during chick rearing. I also found daily shifts in distribution. Murrelets moved between the nearshore and offshore, and in and out of sheltered areas between day and night. I propose that these movements are a result of birds exposing themselves to predation risk in order to forage in areas that are energetically beneficial due to proximity to nest sites or better foraging opportunities.

RÉSUMÉ

J'ai étudié la chronologie et le succès de la reproduction, la distribution et les déplacements d'une population de Guillemot marbré (*Brachyramphus marmoratus*) du détroit Desolation, en Colombie-Britannique, de 1996 à 1998. Cet oiseau de mer (famille des Alcidés) menacé passe la plus grande partie de son temps en mer où il se nourrit de petits poissons. Il se distingue des autres Alcidés en ceci qu'il niche en solitaire dans la forêt ancienne. J'ai recouru à plusieurs méthodes pour étudier la chronologie et la synchronie de la reproduction dans cette population. J'ai utilisé la radiotélémétrie pour établir les taux de survie locale (et les taux d'émigration) des oiseaux de moins d'un an (HY pour *hatch year*) et des oiseaux de plus d'un an (AHY pour *after-hatch year*). J'ai aussi effectué des relevés en mer et utilisé la radiotélémétrie pour étudier les changements à petite échelle dans la distribution spatiale et temporelle des oiseaux en mer.

Les activités de reproduction ont eu lieu à des moments différents d'une année à l'autre (le plus tôt en 1996 et le plus tard en 1998). Les saisons de reproduction étaient longues, avec un chevauchement important des périodes d'incubation et d'élevage des oisillons. En moyenne, la saison de reproduction s'étendait du 21 avril au 5 septembre. L'asynchronisme de la reproduction chez les Guillemots marbrés du détroit Desolation était plus prononcée que celle attendue pour un alcidé à cette latitude.

J'ai calculé les ratios de juvéniles (rapport entre les oiseaux HY et les oiseaux AHY) selon deux méthodes : (1) en utilisant les effectifs des oiseaux HY corrigés en fonction du taux d'émigration et l'effectif moyen des oiseaux AHY pour les périodes de la saison où les dénombrements donnaient les plus grands nombres d'individus (ratio « corrigé »); et (2) en utilisant les dénombrements des oiseaux HY et AHY obtenus durant les mêmes relevés de fin de saison (ratio « concomitant »). Le taux de survie hebdomadaire des oiseaux HY nouvellement pourvus d'un radio-émetteur était de 0,27 (taux d'émigration de 0,73); il était de 0,95 pour les oiseaux AHY (taux d'émigration de 0,05). Le ratio de juvéniles moyen « corrigé » était supérieur ($0,131 \pm 0,053$) au ratio de juvéniles « concomitant » ($0,042 \pm 0,022$), mais inférieur à des estimations indépendantes de la fécondité tirées de données de surveillance des sites de nidification. J'avance que mes estimations du ratio de juvéniles sont inférieures en

raison de différences dans la distribution en mer des adultes et des juvéniles. Il est nécessaire d'interpréter ces estimations avec prudence vu l'ampleur inconnu du biais touchant les effectifs des oiseaux AHY.

Les Guillemots marbrés du détroit Desolation effectuent des déplacements quotidiens et saisonniers liés à la reproduction. Leur densité est habituellement plus élevée dans les zones d'eau froide, mais il arrive qu'ils se rapprochent de la forêt ancienne, particulièrement durant la période d'élevage des petits. J'ai aussi observé des changements journaliers dans leur distribution. Les guillemots passent des eaux côtières à la haute mer et gagnent puis quittent les zones abritées selon qu'il fait jour ou qu'il fait nuit. J'avance que ces déplacements s'expliquent par le fait que les oiseaux, en s'exposant à la prédation, veulent s'alimenter dans des régions énergétiquement avantageuses en ceci qu'elles se trouvent à proximité des sites de nidification et offrent de meilleures possibilités alimentaires.

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General Introduction

Knowledge of the factors that affect timing of breeding, breeding success and habitat choice of individuals is crucial for understanding life history decisions, such as the decision to breed or to forage at a certain location (Birkhead and Harris 1985; Perrins *et al.* 1991).

Birds that produce a single clutch per year should time their breeding activities to be as close as possible to the peak of food availability (Lack 1954), implying population level synchronization of breeding with food abundance. Annual variation in mean lay date in some members of the seabird family Alcidae (which typically produce one clutch per year) is thought to be influenced by changes in food or nest site availability (Birkhead and Harris 1985).

Selection of a habitat by animals is thought to be based on a trade-off between the fitness benefits of the resources in a particular habitat, and the costs associated with occupying that habitat (Fretwell 1972). Changes in preference for a certain habitat might be influenced by factors such as increased energetic demand during the breeding season, which might alter the balance between the costs and the benefits of occupying a habitat (Cairns 1987).

Annual variation in distribution, timing of breeding and reproductive output have been reported in almost all alcids for which successive years of breeding have been studied (Gaston and Jones 1998). It is generally thought that there are increasing degrees of breeding synchrony with latitude, implying that climate is the ultimate limit on breeding season timing and output (Birkhead and Harris 1985; Gaston and Jones 1998). Indirectly, climate affects breeding in alcids through changes in the marine primary production, which influence food availability for seabirds during the breeding season (Hunt and Schneider 1987). Climate directly affects timing of breeding and reproductive output at higher latitudes by physically limiting the start and end of breeding with snow and ice (Birkhead and Harris 1985).

Learning how breeding chronology affects changes in habitat use is essential for understanding life history decisions involving reproduction and habitat selectivity. Knowledge of the behavioural ecology of an animal, its reproductive success and survival, can improve conservation efforts by, for example, improving the accuracy of demographic models and thereby the confidence in conservation decisions (Beissinger 1997), or protecting the appropriate habitat used during crucial stages in the breeding season (Caughley 1994).

In this study, I examined the relationships between breeding chronology, breeding status and habitat selectivity, as well as variation in emigration rates between age classes and estimates of reproductive success of the Marbled Murrelet (*Brachyramphus marmoratus*) at Desolation Sound, British Columbia. The main objectives of my thesis are to: a) describe the breeding chronology of a single population, b) estimate the relative emigration rates of juveniles and

adults, c) correct and evaluate productivity indices, and d) examine the factors affecting the spatial distribution, density and movements of Marbled Murrelets during the breeding season.

The Study Species

Marbled Murrelets are small seabirds of the family Alcidae, which includes the puffins, murrelets, guillemots, and auklets. Unlike most seabirds and unique among other members of its family, Marbled Murrelets are known for nesting solitarily on the mossy branches of old-growth trees, and for their elusive breeding habits (Nelson 1997). Marbled Murrelets spend most of their time at sea, where they feed on a variety of small schooling fish especially Pacific sand lance (*Ammodytes hexapterus*) (Carter and Sealy 1990; Burkett 1995).

Marbled Murrelets are distributed along the Pacific Coast from the Aleutian Islands to central California. The Marbled Murrelet has experienced noticeable declines throughout most of its range (Kelson *et al.* 1995; Piatt and Naslund 1995; U.S. Fish and Wildlife Service 1997). Consequently, the species has been listed as threatened in Canada (Committee on the Status of Endangered Wildlife in Canada) and Washington, Oregon, and California (U.S. Fish and Wildlife Service 1992). California also listed the Marbled Murrelet as endangered under state law in 1997.

The major threats to the Marbled Murrelet are destruction of nesting habitat in old-growth forest, entanglement in gill nets, and oil pollution (Rodway 1990; Rodway *et al.* 1992; Carter and Kuletz 1995; Carter *et al.* 1995; Fry 1995; Nelson 1997; U.S. Fish and Wildlife Service 1997). Anthropogenic threats are likely exacerbated by fluctuations in the abundance of prey resulting from changes in climate and variation in predation rates both on the water and at the nest site. The concern for the loss of murrelet nesting habitat to logging has resulted in most of the research focusing on understanding associations with forest ecosystems. As a result, the relationship between Marbled Murrelets and their marine habitat is poorly understood (Campbell *et al.* 1990; Nelson 1997).

Thesis Organization

The topics addressed in each of the main chapters are closely related, and each builds on the previous ones. In Chapter 1, I describe the breeding chronology of the Marbled Murrelet population at Desolation Sound from 1996 to 1998, derived by integrating data collected by various methods. I examine the biases of each method and test for inter-annual variability in timing of breeding. I also test the hypothesis that Marbled Murrelets are less synchronous breeders than other Alcids, and examine the relationship between latitude and breeding synchrony. Chapter 2 addresses the difficulty of obtaining accurate productivity estimates of this species. I investigate the emigration rates of hatch year birds (HY) and after-hatch year birds

(AHY: adults and subadults) and suggest corrections (that account for emigration rates) to adjust juvenile ratios calculated from HY and AHY birds counted concurrently during at sea surveys. I discuss the accuracy of the resulting juvenile ratios. In Chapter 3, I study small scale (< 100 km) shifts in at-sea distribution and marine habitat selectivity in relation to breeding chronology (using estimates from Chapter 1) and breeding status.

My research is part of a larger project investigating the demography and ecology of Marbled Murrelets in British Columbia. The Marbled Murrelet project is part of the Centre for Wildlife Ecology (CWE, Simon Fraser University, Burnaby, B.C.) led by Dr. Fred Cooke. My thesis chapters include the input from: Lynn Lougheed (capture of Marbled Murrelets, aerial telemetry and estimates of nest success and flyways from nest site monitoring); Brett Vanderkist (sexing of Marbled Murrelets and physiological analysis of egg yolk precursors), and Dr. Sean Boyd (aerial telemetry).

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Chapter 1. The Breeding Chronology of Marbled Murrelets in Desolation Sound, British Columbia.

Abstract. I used several methods to study the chronology and synchrony of breeding events of the Marbled Murrelet (*Brachyramphus marmoratus*) population at Desolation Sound, British Columbia, from 1996 to 1998. The timing of breeding events varied among years; on average the breeding season was from April 21 to September 5. In general, breeding synchrony in alcids increased with latitude (41.4% of the variation was explained by latitude). Marbled Murrelets, however, bred more asynchronously than predicted for an alcid at this latitude (50°N). I assessed the biases of each method used by comparing the results to the estimate of the integrated breeding chronology. Counts of hatch year (HY) birds at sea were biased toward earlier breeders, missing an estimated 24% of the fledging events. Physiological analysis of the yolk precursor vitellogenin from blood samples and telemetry monitoring could produce a complete distribution of breeding events if sampling were done throughout laying. Observations in the forest, first observation of a fledgling at-sea during the breeding season, and fish-holding behaviour produced insufficient data to be used as sole indicators of breeding chronology.

Introduction

Details of the breeding chronology of a species and its variability are crucial to understanding strategic life history decisions and environmental influences on reproduction (Birkhead and Harris 1985; Perrins *et al.* 1991). Most research on the timing of breeding in seabirds has been conducted on land at breeding colonies where large samples can be obtained year after year (Gaston and Jones 1998). Unlike most seabirds and unique among other members of their family (the Alcidae), Marbled Murrelets (*Brachyramphus marmoratus*) are known for nesting solitarily on the mossy branches in old-growth trees, and for their elusive breeding habits (Nelson 1997).

Their cryptic nesting behaviour makes the Marbled Murrelet a difficult species to study, constraining the amount and type of information collected (Nelson and Hamer 1995; Ralph *et al.* 1995; Nelson 1997). Due to difficulties in data collection, sample sizes have been small and chronology estimates have been largely based on incidental or fortuitous observations pooled over several locations and years (see Carter and Sealy 1987; Hamer and Nelson 1995; Nelson 1997). Consequently, the characteristics of the Marbled Murrelet breeding phenology and breeding biology have remained as significant gaps in our knowledge of the life history of this threatened species. I studied the breeding chronology of the Marbled Murrelet population at Desolation Sound, British Columbia during three breeding seasons. Each year, I integrated data from several methods. I examined potential biases of these methods and their effects on the interpretation of the results. I also examined the interannual variability in timing of breeding.

Marbled Murrelets are thought to be more asynchronous in breeding than other Alcids, perhaps because of their solitary nesting habits (Hamer and Nelson 1995). I tested the hypothesis,

within a single population, that Marbled Murrelets are less synchronous breeders than other Alcids, and examined the relationship between latitude and breeding synchrony.

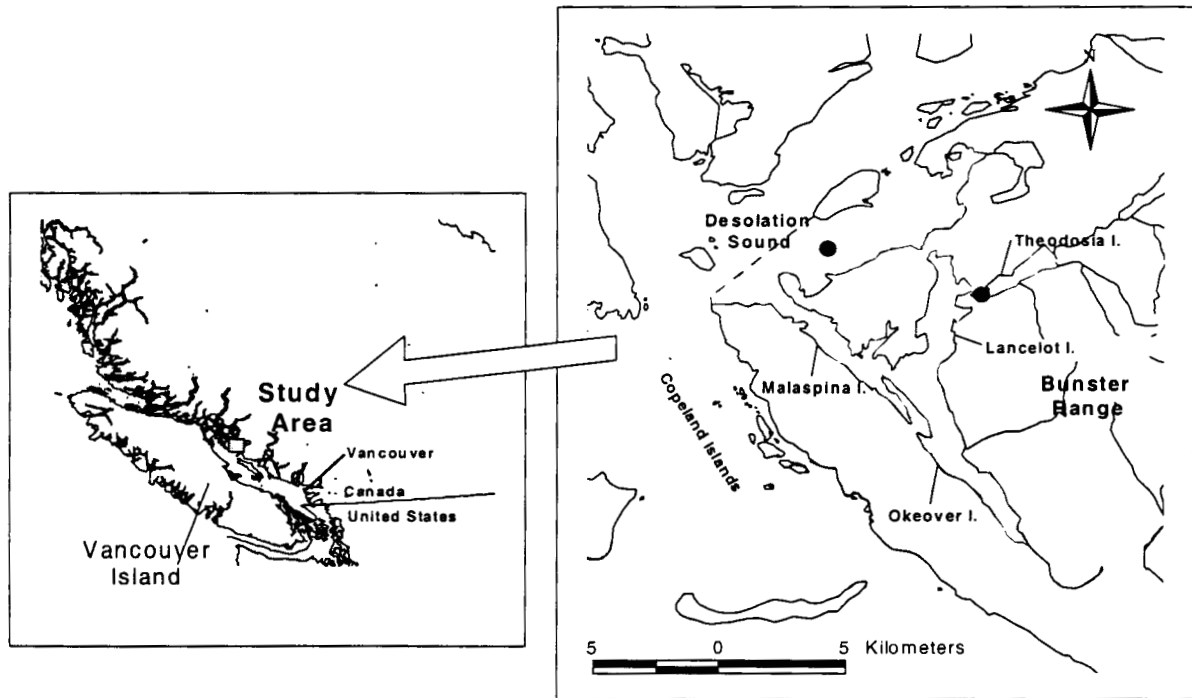
Methods

Fieldwork was conducted in Desolation Sound from 1996 to 1998 (Fig. 1.1). Data on egg laying, hatching and fledging were collected using several methods including at-sea surveys, physiological analysis, radio telemetry, and observations in the forest.

The survey area included the southern portion of Desolation Sound (between 50° 04'N, 124° 50'W and 50° 07'N, 124° 44'W) and the adjacent glacial fjords (Malaspina, Lancelot, Okeover and Theodosia Inlets; Fig. 1.1). At-sea surveys were conducted from a 4.5-m hard shell inflatable boat in 1996 and 1997, and from a comparable 5.2-m fiberglass boat in 1998 following a standardized strip transect protocol with one driver and 2 observers, one on each side of the vessel (RIC 1995). Survey route was followed by means of a Global Positioning System. At-sea surveys were conducted between May and mid-August each year, after which time hatch year (HY) birds cannot be accurately differentiated from after-hatch year (AHY) birds due to AHY birds moulting into basic (winter) plumage (Carter and Stein 1995). Observations of AHY birds entering advanced body moult and starting wing moult were used as clues to end the surveying period. Surveys were cancelled during rain or rough sea conditions (beyond 2 on the Beaufort scale). Totals of 24, 23 and 17 surveys were completed during the 1996, 1997, and 1998 breeding seasons, with an average time between surveys of 4, 4 and 6 days, respectively (range 1 - 12 days). Observers recorded the presence of murrelets holding fish. Following Sealy (1974), I used the initiation of fish-holding behaviour, which implies that adults are feeding nestlings, as direct evidence of the beginning of hatching. Observers also recorded plumage of murrelets encountered: juvenile or alternate (breeding) plumage, and evidence of body or wing moult. Because of limited knowledge of fledgling emigration rates at sea, previous chronology studies have used only the first hatch year (HY) observation of the season as an indication of the beginning of fledging (Hamer and Nelson 1995). I used all the sightings of HY birds throughout the season after correcting for emigration rate. This correction takes into account the number of juveniles that may have stayed from the previous survey (that did not emigrate), therefore only 'new' (not counted previously) HY birds are included in the sample. In Desolation Sound, 17% of HY birds were estimated to disperse from the survey area daily (for details on HY count corrections see Chapter 2).

Egg laying dates for captured female Marbled Murrelets were estimated by measuring the levels of vitellogenic zinc (VTG-Zn) in the plasma. Marbled Murrelets were captured between June 6

Figure 1.1. Map of Desolation Sound, British Columbia. Solid circles show the main capture areas for night-lighting in Desolation Sound, and mist-netting in Theodosia Inlet. The survey area is shaded in gray.



– August 6 in 1996 and May 14 – August 11 in 1997 at Theodosia Inlet by mist-netting (technique described in Kaiser *et al.* 1995). Murrelets were also captured in Desolation Sound from May 14 – June 19 and from July 3 – August 7 by night-lighting (modified from Whitworth *et al.* 1997). VTG-Zn is an indirect measure of the yolk precursor VTG (Mitchell and Carlisle 1991). Marbled Murrelets with levels of VTG-Zn ≥ 0.61 ug/ml VTG-Zn are thought to be egg-producing (Vanderkist 1999). Vanderkist (1999) used Cassin's Auklets (*Ptychoramphus marmoratus*) to validate the technique of using VTG-Zn as indicators of fecund Marbled Murrelets because they are similarly sized Alcids, they lay one egg and both breeding chronology and the process of egg-formation (Astheimer 1986) are known. Assuming that egg-formation in Marbled Murrelets is similar to that of Cassin's Auklets, and takes about 14 days (Astheimer 1986), and that captured female murrelets with elevated VTG-Zn were on average half-way through the egg-forming process (7 days of egg production), 7 days was added to the capture date of birds showing elevated levels of VTG-Zn to estimate lay date.

Telemetry transmitters were used on 40 Marbled Murrelets to locate nests and study activity patterns of nesting birds in 1998. Murrelets were captured by night-lighting from May 4 – May 18. Transmitters were attached using a sub-dermal anchor modified from the technique of Newman *et al.* (in press), but I used epoxy glue (Bird Adhesive, Titan Corporation, USA) instead of a suture to secure the device. Telemetry transmitters were manufactured by ATS (Advanced Telemetry Systems, Isanti, MN 55040 USA), Model 394, weighing 2.0 g and with a battery life of 45 days. I radio-tracked the birds every day, weather permitting, by boat, helicopter or both. I tracked the daily patterns of presence or absence of radioed birds on the water to detect changes due to incubation shifts following egg laying. Marbled Murrelets have 24-hour incubation shifts, with one adult brooding while the other forages at sea (Simons 1980; Hirsch *et al.* 1981; Nelson and Peck 1995). I defined egg laying date as the date when a breeding bird equipped with a radio transmitter started to show a daily "on-off" pattern at sea.

Observations from active nests located using a combination of dawn activity surveys and tree climbing in old-growth forest adjacent to Desolation Sound, 4 in 1996 (Manley 1999) and 3 in 1998, were also incorporated into the estimates of breeding chronology. Because these nests were found at different stages of the breeding cycle, I was only able to estimate intervals for hatching, fledging, incubation or chick rearing, except for one nest for which fledging date was determined.

Breeding Chronology

I estimated the breeding chronology for each year of the study by pooling data from all the methods used that year, and the overall breeding chronology by averaging results from the three years. Incubation was defined as the interval from the first detection of laying to the last detection of hatching, and chick rearing as the interval from the first detection of hatching to the last detection of

fledging. Because Marbled Murrelets breeding was asynchronous (see results), with incubation and chick rearing spread over a long period, I also estimated core incubation and core chick rearing periods for each year. The “core periods” were estimated as the middle 50% of the frequency distribution for incubation or chick rearing. Each of the methods described above produced information on laying, hatching or fledging events, except for some of the forest observations. The unknown events for each known event, were extrapolated assuming a 30-day incubation period and a 28-day nestling period, following Carter and Sealy (1987) and Hamer and Nelson (1995), to allow comparisons with other studies.

Comparing Methods

I compared laying, hatching and fledging periods separately by method and by year to detect potential biases in each method. For methods that produced frequency distribution data, I compared the fledging dates, with one-way analysis of variance (ANOVA) on \log_{10} transformed data of: (1) corrected juvenile counts from at-sea surveys vs. physiological analysis of VTG-Zn for 1997, and (2) corrected juvenile counts from at-sea surveys vs. radio-telemetry for 1998.

I calculated the proportion of fledging events that were likely missed during the surveys in 1997 at the end of the season. Two methods that produced frequency distribution data for the whole breeding season were available (at-sea surveys and VTG-Zn analysis). I compared the date of the last at-sea survey to the estimated distribution of fledging, and calculated the proportion of fledging events that could potentially have been seen by the surveyors after this period.

Interannual Variability

Interannual variability among 1996, 1997 and 1998 was evaluated in two ways: (1) by comparing the mid-points of the range of breeding season dates, and (2) by comparing the timing of fledging of juveniles from at-sea survey counts. Although at-sea surveys did not sample the end of the fledging season, they were conducted at equivalent periods each year of the study; from the appearance of the first HY bird until the adults began to moult. Differences in the timing of fledging were tested with one-way ANOVA on \log_{10} transformed data of HY bird counts corrected for juvenile dispersal. Pairwise comparisons were done with a post-hoc Student Newman-Keuls test (SNK).

Breeding Synchrony

I tested for relationships between latitude and synchrony among all members of the family Alcidae with univariate least squares linear regression models using the range of laying dates (from the day that the first egg is detected to the date that the last egg is detected). I chose to use the range of laying dates because it is the most commonly reported statistic of breeding synchrony in the literature. Details of the data selection are in Appendix 1.1. To determine if breeding synchrony of Marbled

Murrelets is different from that of other Alcidae, I compared my estimate of the range of laying dates to the 95% confidence intervals around the predicted value from the regression of range of laying dates of other alcids on latitude (Sokal and Rohlf 1981). I looked for an effect of taxonomic position on breeding synchrony by comparing the means of laying date ranges within sub-families of Alcids with one-way ANOVA. My taxonomy follows Strauch (1985).

All statistical analyses were done with SAS (SAS Institute 1996). Dependent variables were first tested for normality using Shapiro-Wilk tests and were \log_{10} transformed prior to analyses if necessary (Sokal and Rohlf 1981). Values are reported as mean \pm SE unless otherwise indicated. Statistical significance was accepted at $P \leq 0.05$.

Results

Surveys at Sea

Surveys at sea were done from May 14 – August 14 in 1996, May 11 – August 5 in 1997 and May 6 – August 12 in 1998. Fish-holding behaviour was first detected on June 1 in 1996, May 24 in 1997 and June 7 in 1998 (Table 1.1). HY birds were observed from June 25 – August 14 in 1996, June 27 – August 5 in 1997 and June 11 – August 12 in 1998. The ending of observations of HY birds reflect the end of the surveying period (Table 1.1). Totals of 159, 38 and 29 HY Marbled Murrelets were counted during surveys in 1996, 1997, and 1998. Totals of 67, 21 and 20 “new” juveniles were estimated after correcting the number of observed HY birds for the daily rate of emigration (see Appendix 2.1, Chapter 2). The proportion of fledging events missed by at-sea surveys at the end of the fledging period was approximately 24%.

Physiological Analysis: 1996 and 1997

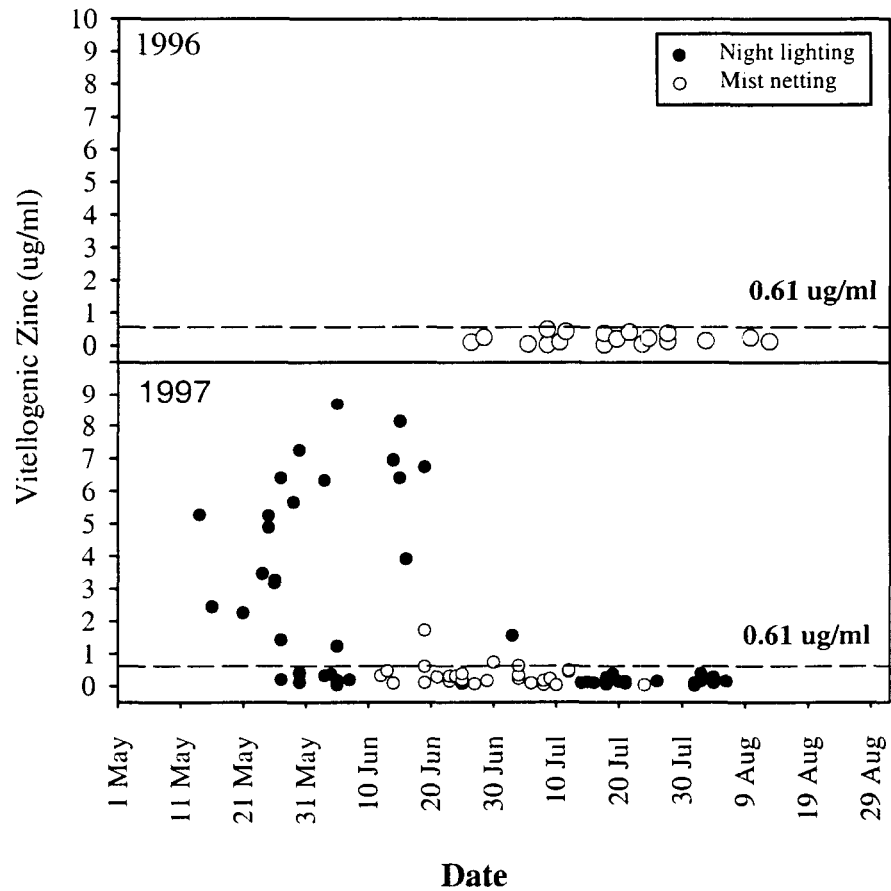
No egg-producing females were detected from the 1996 mist-net samples ($0.18 \pm 0.15 \mu\text{g/ml}$, $n=24$), and only two egg-producing females were detected from the 1997 mist-net samples ($0.18 \pm 0.29 \mu\text{g/ml}$, $n=52$, Fig. 1.2). In 1997, 21 egg-producing females were captured by night-lighting ($1.93 \pm 2.66 \mu\text{g/ml}$, $n=55$, Fig. 1.2); 20 in the first capture period (May 14 – June 19) and 1 on July 3 in the second capture period (July 3 – August 7). Unfortunately, no samples were available from June 20 – July 2, 1997 due to decreased night-lighting effort. The laying period estimated from analysis of VTG-Zn during 1997 was from May 21 – July 10 (Table 1.1).

Table 1.1. Laying, hatching and fledging dates estimated by several methods for 1996, 1997 and 1998. The data used to infer the breeding chronology for each method are in bold. Data from the forest for 1996 and 1998 represent the range estimated from all the observations. Only the start of laying and the start of fledging were extrapolated from the first observation of fish-holding behaviour each year because n=1; -- = not estimated.

Year	Method	Laying		Hatching		Fledging		n
		Start	End	Start	End	Start	End	
1996	Fish-holding	2 May	--	1 Jun	--	29 Jun	--	1
	HY Counts at Sea	28 Apr	17 Jun	28 May	17 Jul	25 Jun	14 Aug	67
	Forest ^a	12 May	19 Jul	11 Jun	18 Aug	16 Jul	15 Sep	4
1997	Fish-holding	24 Apr	--	24 May	--	21 Jun	--	1
	HY Counts at Sea	30 Apr	8 Jun	30 May	8 Jul	27 Jun	5 Aug	21
	VTG-Zn	21 May	10 Jul	20 Jun	9 Aug	18 Jul	6 Sep	23
1998	Fish-holding	8 May	--	7 Jun	--	5 Jul	--	1
	HY Counts at Sea	14 Apr	15 Jun	14 May	15 Jul	11 Jun	12 Aug	20
	Telemetry	11 May	19 Jun	10 Jun	19 Jul	8 Jul	16 Aug	24
	Forest	1 Jun	30 Jun	1 Jul	30 Jul	29 Jul	27 Aug	3

^a Manley (1999).

Figure 1.2. VTG-Zn vs. capture date for Marbled Murrelets captured at Desolation Sound in 1996 (top) and 1997 (bottom). Birds captured by mist netting are represented by open circles, and birds captured by night-lighting by solid circles. VTG-Zn egg-producing limit marked with broken lines (for details see Vanderkist 1999).



Radio Telemetry: 1998

Twenty-three active nests were located from birds with telemetry transmitters. At one of these nests both members of the pair had been radio tagged (24/40 breeding birds). These birds started incubation between May 11 and June 19 (Table 1.1). On average birds started incubation 12.65 ± 9.56 days ($n=24$) after capture, except for one bird that may have already been incubating when captured.

Forest Observations

Of the 7 active nests found by dawn activity surveys and tree climbing, one (in 1998) was monitored around fledging, and fledging date was determined. Of the 6 other nests, 3 were monitored before and after hatching or fledging. For these, I estimated a hatching or fledging “interval”. The remaining 3 nests were monitored only during incubation or chick rearing (Table 1.1).

Breeding Chronology

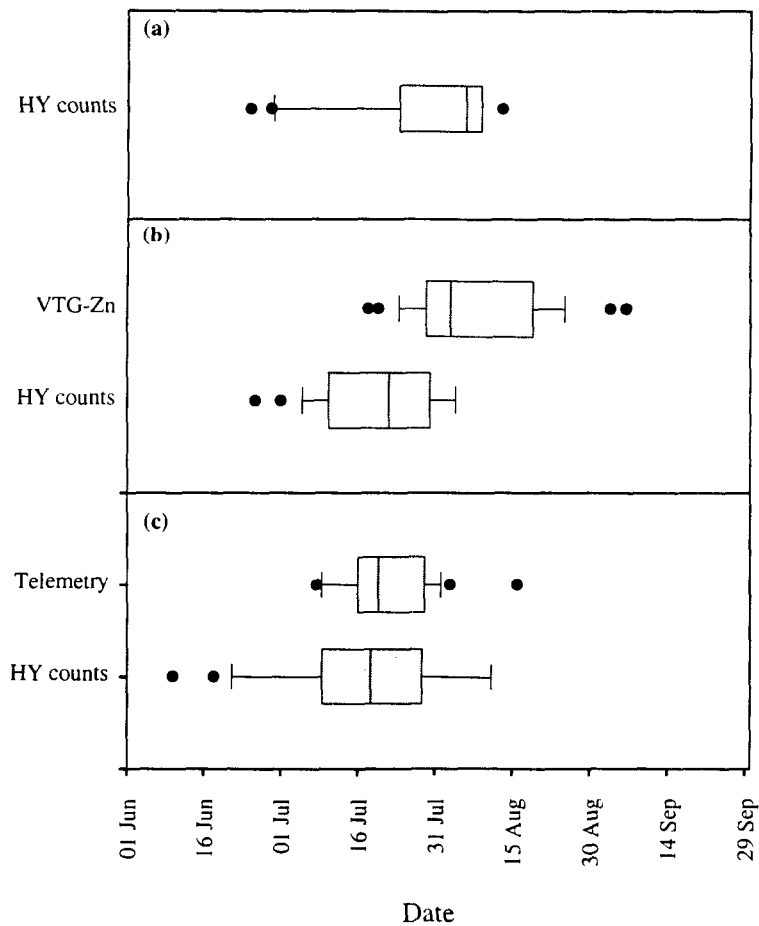
Chronology estimates varied by method (summarised in Table 1.1). This variability could have been due to chance variation or bias. The beginning of laying, hatching and fledging periods predicted from the initiation of fish-holding behaviour each season were similar to the estimates from HY survey counts for 1996 and 1997 but not for 1998 when initiation of fish-holding occurred later.

Chronology estimates derived from HY counts at-sea and VTG-Zn analysis for 1997 were significantly different ($F_{1,42} = 25.37$, $P < 0.01$). Data from HY counts suggested an earlier breeding period than that derived from VTG-Zn data (Fig. 1.3b). The median fledging date was July 22 for HY bird counts, and August 3 for VTG-Zn, with a 17-day overlap between the two. Pooling both methods, the median fledging date was July 30.

There were no significant differences between chronologies derived from HY counts at sea and radio-telemetry data from 1998 ($F_{1,42} = 1.94$, $P=0.17$, Fig. 1.3c). The median fledging date was July 19 for HY counts at-sea, and July 20 for radio-telemetry, however, the breeding period derived from radio-telemetry started and ended later than the breeding period derived from HY bird counts at sea. Breeding intervals calculated from observations of active nets in 1996 and 1998 both suggested later breeding compared to the other methods (Table 1.1).

The murrelet breeding season in Desolation Sound, derived from integrating results from all the methods, ranged from April 28 to September 15 in 1996 (140 days), from April 24 to September 6 in 1997 (135 days), and from April 14 to August 27 in 1998 (135 days), with a three year average of

Figure 1.3. Fledging dates derived from: (a) HY counts at sea ($n = 67$) from 1996 (b) HY counts at sea ($n = 21$) and egg-producing females from VTG-Zn analysis ($n = 23$) for 1997, and (c) HY counts at sea ($n = 20$) and radio telemetry ($n = 24$) for 1998. Time of fledging was significantly different between HY counts and VTG-Zn analysis, but not significantly different between HY counts and radio telemetry methods ($F_{1,42} = 25.37, P < 0.01$; $F_{1,42} = 1.94, P = 0.17$). Time of fledging from HY counts at sea for the three years of the study were significant differences between years ($F_{2,105} = 9.36, P < 0.01$). Plots show the median, 10th, 25th, 75th, 90th percentiles and outliers.



137 days. There was an overlap of 79 days on average between incubation and chick rearing, but the overlap was only 20 days for the core periods (Table 1.2).

Interannual Variability

The comparison of the mid-points of the breeding seasons showed a trend for increasingly earlier breeding, from July 7 in 1996 to June 30 in 1997 and June 20 in 1998. Timing of fledging varied significantly among years ($F_{2,105} = 9.36$, $P < 0.01$). Fledging was latest in 1996, followed in order by 1997 and 1998 (Fig. 1.3a). Pairwise comparisons were significant between 1996 and 1997, 1996 and 1998 but not between 1997 and 1998 (SNK test).

Breeding Synchrony

Breeding synchrony in Alcids was related to latitude; 41.4% of the variation in range of laying dates was explained by latitude (range = -0.93 (latitude) + 86.7, $r^2 = 0.414$, $P < 0.05$; Fig. 1.4). Marbled Murrelets laying range was 79 days based on the three-year average, which is greater than the predicted value for an alcid at this latitude (50° N), and fell outside the 95% confidence intervals. Laying dates did not differ significantly between sub-family groups ($F_{4,17} = 1.24$, $P = 0.332$).

Discussion

Breeding Chronology

Breeding season of Marbled Murrelets in Desolation Sound was on average from April 21 to September 5. The duration of the breeding season was longer and with a greater overlap between incubation and chick rearing than previously reported for British Columbia; 118 days (Hamer and Nelson 1995) compared to my 137-day average. The core incubation and core chick rearing periods had a smaller overlap than the whole range, with core incubation occurring mostly in June and core chick rearing occurring mostly in July.

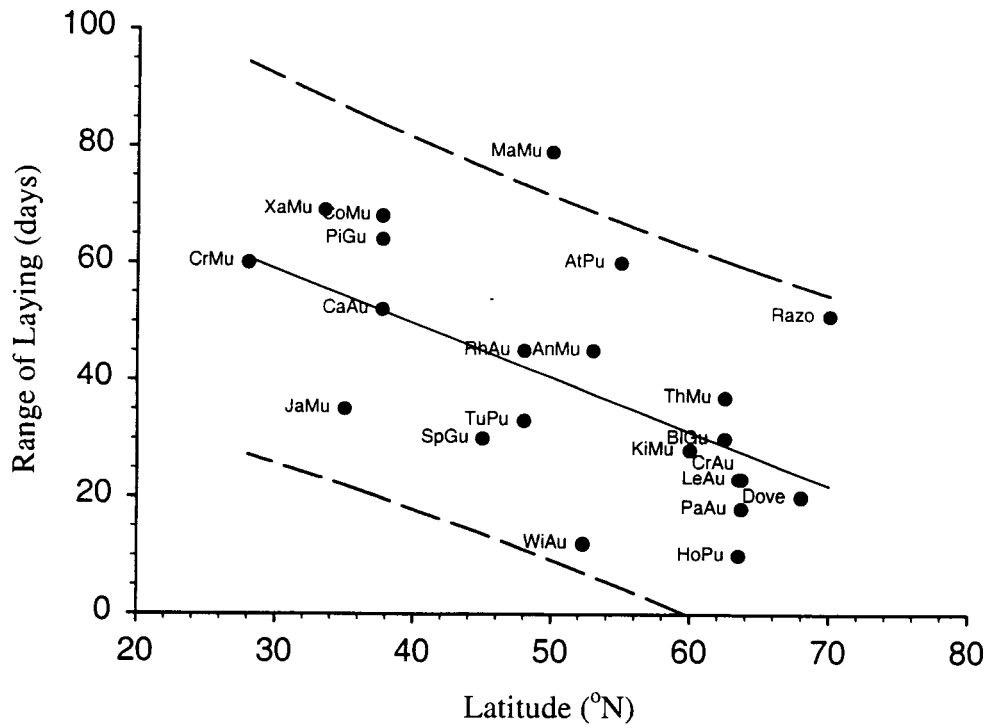
Interannual Variability

The duration of the breeding season was broadly consistent among years, but there was a trend towards increasingly earlier breeding from 1996 to 1998. In addition, mean fledging, as measured by HY counts at sea, occurred significantly later in 1996 than in 1997 and 1998, with no differences between 1997 and 1998. Changes in the marine environment affect breeding decisions of seabird communities (Nelson 1997; Gaston and Jones 1998). This trend of earlier breeding for the murrelet

Table 1.2. Incubation and chick rearing periods, with core periods, for Desolation Sound during the 1996, 1997 and 1998 breeding seasons.

Year	Incubation				Chick rearing			
	Range	Duration (days)	Core (middle 50%)	Duration (days)	Range	Duration (days)	Core (middle 50%)	Duration (days)
1996	28 Apr – 18 Aug	112	24 May – 12 Jul	49	28 May – 15 Sep	110	23 Jun – 9 Aug	47
1997	24 Apr – 9 Aug	107	22 May – 9 Jul	48	24 May – 6 Sep	105	21 Jun – 6 Aug	46
1998	14 Apr – 30 Jul	107	13 May – 3 Jul	51	14 May – 27 Aug	105	12 Jun – 29 Jul	47
Average	22 Apr – 8 Aug	109	19 May – 8 Jul	49	22 May – 5 Sep	107	18 Jun – 4 Aug	47

Figure 1.4. Range of laying (days) vs. latitude for the 22 members of the Alcidae family showing the regression line (solid line) with the 95% CI (broken line). Marbled Murrelets' laying range falls outside the 95% CI. (see appendix 1.1 for details of data selection).



population in Desolation Sound coincides with significant interannual increases of sea-surface temperature during the breeding season in the study area. Sea-surface temperature was lower in 1996 than in 1997 and 1998 (Chapter 3).

Comparing Methods and Their Biases

The estimation of breeding chronology by method and by year using data collected from within one population permitted the assessment of biases and limitations in each method. Some estimates of breeding chronology, calculated using two different methods for the same year, produced different results in terms of length and timing of breeding, however, the biases in some instances were methodological and could be overcome in future studies. Methods that produce large sample sizes and frequency distribution of the breeding events such as physiological analysis (i. e., VTG-Zn), telemetry monitoring of breeding activities, and HY counts at sea, conducted throughout the breeding season, are preferred over methods that produced a few scattered data points. Other methods such as the first fish-holding event, the first sighting of a juvenile at sea, and various types of forest observations are less desirable because they are limited by small sample sizes within a single breeding season, and only permit researchers to estimate ranges of breeding dates. However, these methods are still of value because in many cases they are the only information available for a basic understanding of the breeding chronology in an area (for examples see Hamer and Nelson 1995; Nelson and Peck 1995; Manley 1999).

Estimates of initiation of the breeding periods were similar for fish-holding behaviour and HY count data, except for 1998 when fish-holding estimates were 25 days later than those from HY counts (Table 1.1). In Theodosia Inlet, the number of birds holding fish increased at dusk (P. Dehoux, unpub. data), and other studies have found that murrelets feed chicks mostly at dawn and dusk (Carter and Sealy 1990; Nelson 1997). In 1998, surveys were only done in the morning, so fish-holding behaviour may have been missed. The use of the start of fish-holding behaviour as an indicator of hatching relies on the assumption that birds are using the monitored area as their primary feeding area during that stage of the breeding season.

The chronologies estimated from HY counts and from VTG-Zn analysis are biased in opposite directions. The breeding season estimated from survey counts starts and ends earlier than that estimated from VTG-Zn analysis (see Fig. 1. 3). The bias from the VTG-Zn analysis was methodological; egg producing females were detected since the first day of capture, earlier evidence of egg producing may have been detected had the captures by night-lighting started earlier. This bias could be avoided if capture and blood sampling was conducted throughout the laying period. The fact that at-sea surveys cannot be conducted once AHY birds have started their pre-basic molt truncates the data set, missing about an estimated 25% of the fledging events. This explains the apparent earlier

ending of the breeding season in all years, however, due to the consistency of the method, it allows for interannual comparisons.

Because HY counts were biased towards the early part of the breeding season, and there were no significant differences between telemetry and HY counts estimates (see Fig. 1.3), I suggest that radio telemetry in 1998 was similarly biased. The fact that radio transmitters were deployed on birds only early in the season and not throughout the laying period may have biased the sampling towards earlier breeders.

The breeding estimates from forest observations in 1996 and 1998 were the latest (September 15), overall 9 days later than the latest breeding date estimated from VTG-Zn. Manley (1999) speculated that the 1996 bird might have re-nested based on earlier evidence of breeding at the same site.

Individual variation in the length of incubation and nestling periods may affect my estimates of breeding chronology. In other alcids, the length of incubation and nestling periods varied among years and within seasons (Ainley and Boekelheide 1990). For the few Marbled Murrelet nests monitored throughout the years ($n = 4$), incubation varied from 28-30 days and nestling 27-40 days (Simons 1980; Hirsch *et al.* 1981; Nelson and Peck 1995), but to allow comparisons with other studies, I assumed a 30-day incubation period and a 28-day nestling period (Carter and Sealy 1987; Hamer and Nelson 1995).

Breeding Synchrony and Duration

My analyses indicates that Marbled Murrelets are significantly more asynchronous than predicted at this latitude, based on the measured synchrony of other Alcidae. The decision to breed is generally thought to be state dependent (McNamara and Houston 1996). An individual's state is determined by the underlying physical and environmental condition that determine its survival or its ability to reproduce. Marbled Murrelet breeding asynchrony might be a response to the seasonal (temporal) availability of prey. The relationship between Marbled Murrelet prey availability and reproductive success is unknown (Burkett 1995). It is also possible that breeding asynchrony in Marbled Murrelets is related to their solitary nesting behaviour. Seabird colonies are generally viewed as information centres where seabirds receive clues from neighbours regarding the locations of foraging areas (Kaiser 1994). Therefore, being synchronized with neighbours during the breeding season becomes important. Being non-colonial, the need for murrelets to exchange information at the nest site becomes irrelevant and so would the need to be synchronized. Kaiser (1994) suggests that Marbled Murrelet's inland nesting habits allows them to take advantage of high prey concentrations in the coastal fjords during the summer and relates these to the evolution of solitary nesting in this species.

The same pattern of shorter breeding seasons with increasing latitude has been observed in Marbled Murrelets, with the longest and earliest breeding seasons in California, and the shortest and latest in Alaska (Carter and Sealy 1987; Hamer and Nelson 1995). The latter may explain the difference between my estimates of the duration of the breeding season and the estimate for British Columbia reported by Hamer and Nelson (1995), which was based mostly on data collected at higher latitudes.

Understanding the basic characteristics of the breeding biology of Marbled Murrelets, such as breeding chronology, should assist in evaluating the significance of behaviours, activity patterns or habitat use with respect to the breeding cycle. Although I found evidence suggesting that breeding seasons are occurring earlier, more data are required to confirm this trend, and it should be carefully scrutinized over a longer period. A long-term data set is needed to better understand how variation in ocean conditions, climate and prey abundance affect timing of breeding of this threatened species.

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Appendix 1.1. Reported range of laying (in days) of Alcidae and latitude of the study. If more than one year was reported, then the mean range of all the years for which data were available was used (see the notes section for years used). In some cases, such as the Common Murre, several years of data were available for several colonies at different latitudes. I chose to use data from the study that reported the most years of complete ranges of laying dates. In other cases, data were sparse, so I used estimates from Gaston and Jones (1998), and is indicated by “approx.” in the notes. If a range of dates was reported, I used the midpoint. Lay dates that were indicated to be re-nesting were excluded, to make the all data comparable. Sub-family and species names are as in Table 2 of Gaston and Jones (1998), based on Strauch (1985).

Subfamily	Species	Code	Latitude (°N)	Days of Laying	Source	Notes
Aethini	Cassin's Auklet	CaAu	37.7	52	Ainley <i>et al.</i> (1990)	1970-1983
Aethini	Parakeet Auklet	PaAu	63.7	18	Sealy (1975)	
Aethini	Least Auklet	LeAu	63.7	23	Bedard (1969)	
Aethini	Whiskered Auklet	WiAu	52.3	12	Knudtson and Byrd(1982)	
Aethini	Crested Auklet	CrAu	63.5	23	Piatt <i>et al.</i> (1990)	
Alcini	Dovekie	Dove	68	20	Gaston and Jones(1998)	Approx.
Alcini	Razorbill	Razo	70	51	Paludan (1947)	
Alcini	Common Murre	CoMu	37.7	68	Boekelheide <i>et al.</i> (1990)	1972-1983
Alcini	Thick-billed Murre	ThMu	62.5	37	Gaston and Jones (1998)	
Brachyramphini	Kittlitz's Murrelet	KiMu	60	28	Day (1996)	
Brachyramphini	Marbled Murrelet	MaMu	50	79	This study	
Cepphini	Black Guillemot	BiGu	62.5	30	Gaston and Jones(1985)	
Cepphini	Pigeon Guillemot	PiGu	37.7	64	Ainley <i>et al.</i> (1990)	1971-1982
Cepphini	Spectacled Guillemot	SpGu	45	30	Gaston and Jones (1998)	Approx.
Cepphini	Xantus' Murrelet	XaMu	33.5	69	Murray <i>et al.</i> (1983)	
Cepphini	Craveri's Murrelet	CrMu	28	60	Gaston and Jones(1998)	Approx.
Cepphini	Ancient Murrelet	AnMu	53	45	Gaston and Jones (1998)	
Cepphini	Japanese Murrelet	JaMu	35	35	Gaston and Jones (1998)	Approx.
Fraterculini	Rhinoceros Auklet	RhAu	48	45	Gaston and Jones (1998)	
Fraterculini	Tufted Puffin	TuPu	48	33	Burrell (1980)	
Fraterculini	Atlantic Puffin	AtPu	55	60	Harris (1984)	
Fraterculini	Horned Puffin	HoPu	63.7	10	Sealy (1973)	Small sample

**Chapter 2. Local Survival of Adult and Juvenile Marbled Murrelets and their Importance
for Estimating Reproductive Success.**

Abstract.- Juvenile ratios from numbers of hatch year (HY) and after-hatch year (AHY) Marbled Murrelets (*Brachyramphus marmoratus*) counted concurrently during at-sea surveys are commonly used to estimate fecundity in this species. These “concurrent” juvenile ratios assume that HY birds remain in an area, and are likely biased because they do not account for differences in emigration rate of HY and AHY birds. I studied the emigration rates of adult and juvenile Marbled Murrelets marked with radio transmitters in Desolation Sound, British Columbia, and calculated juvenile ratios considering movement. Juveniles had a high emigration rate compared to adults. The weekly local survival rate (ϕ) of newly radio-tagged HY birds was 27%, with a minimum average residence time of 5.3 days, and a weekly emigration rate ($1-\phi$) of 73%. AHY local survival was high, 95% during incubation and early chick rearing, suggesting that the population of murrelets during the breeding season is resident. I calculated juvenile ratios from 1996 – 1998 using: (1) HY counts corrected for emigration and mean AHY counts around the breeding season peak, and (2) HY and AHY counts from concurrent at-sea surveys. The average “corrected” juvenile ratio in Desolation Sound was higher (0.131 ± 0.053), than the “concurrent” juvenile ratio (0.042 ± 0.022) but lower than estimates of fecundity from nest monitoring (0.16 – 0.46). Low juvenile ratios from at-sea surveys could result either from an unknown proportion of non-breeding age birds (subadults) in the population, or, more likely, from differences in the at-sea distribution of AHY and HY birds. Fluctuation in the timing of the peak number of AHY birds across years might result in an uncorrectable bias in the counts. Accurately estimating the number of AHY birds is essential for the calculation of representative juvenile ratios. Because of biases and potential problems, caution is needed when interpreting juvenile ratios from at-sea surveys.

Introduction

The conservation of Marbled Murrelet (*Brachyramphus marmoratus*) populations is a concern over its entire range, especially in Oregon, Washington, and British Columbia where the species has been designated threatened (Rodway 1990; Rodway *et al.* 1992; U.S. Fish and Wildlife Service 1992) and California, where the species is listed as endangered (U.S. Fish and Wildlife Service 1997). All changes in population size result from changes in vital rates (births, deaths, emigration, or immigration) (Caswell 1989). Conservation measures are usually more effective and reliable with knowledge of the demography of a population, especially the vital rates (Caughley 1994). Although none of these rates are known with any certainty for any Marbled Murrelet population, monitoring of fecundity (births) has been identified as a priority, because, according to existing data, it is thought to be low (Beissinger 1995).

Accurate estimates of fecundity are essential for demographic population modeling (Caswell 1989). Fecundity is defined as the number of female offspring per breeding age female (Caswell 1989), but is commonly measured as some form of general reproductive success, such as the number of fledglings per breeding adult or per nest. Marbled Murrelets are atypical members of the family Alcidae in that their nests are relatively widely dispersed and usually found high in trees in old-growth, coastal forests (Nelson and Hamer 1995; Nelson 1997). The inaccessibility of their nests and their cryptic behaviour make unbiased measurements of Marbled Murrelet reproductive success from nest observations very difficult and expensive at best (Nelson and Hamer 1995). Monitoring reproductive success of this species is important, therefore, alternate indices of fecundity are needed. The most commonly used method is a calculation of the proportion of hatch year (HY) to after-hatch year (AHY) birds counted concurrently during surveys at sea, usually called either “juvenile to adult” or “juvenile” ratios (Beissinger 1995; Ralph and Long 1995; Strong *et al.* 1995; Kuletz and Kendall 1998). Juvenile ratios have been assumed to be an index of fecundity (productivity indices) because they approximate the proportion of juveniles per adult. Non-breeding age AHY birds (subadults, birds too young to breed), have the same plumage as breeding age AHY birds (potential breeders) and they can not be separated in counts at sea, therefore, the juvenile ratios are not true fecundity but an index of productivity.

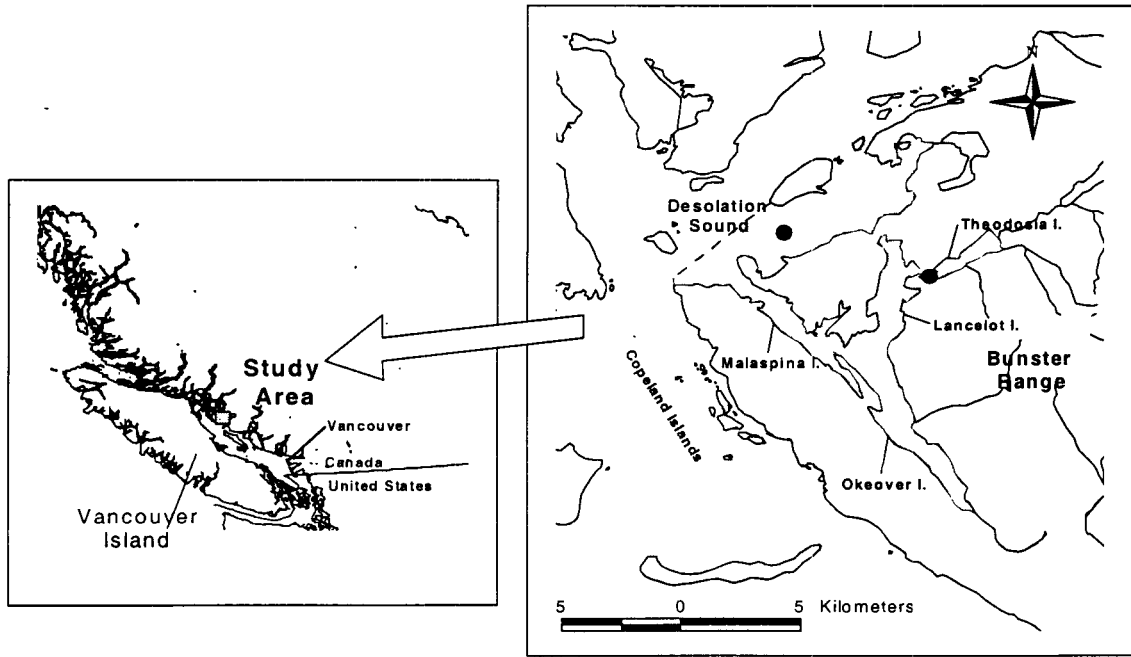
Juvenile ratios from concurrent at-sea surveys are likely biased (Beissinger 1995; Kuletz and Kendall 1998) because they do not account for immigration or emigration rates of HY and AHY birds. Pilot work at the study site in 1997 suggested that juveniles move out of the survey area at a high rate, and that adults emigrate as the end of the breeding season approaches (Lougheed and Lougheed 1998). Differential turnover of the two age classes (AHY and HY) could lead to biases in the observed juvenile ratio (Beissinger 1995; Kuletz and Kendall 1998).

The objectives of this study were: (1) to estimate the local survival (and emigration rates) of HY birds after fledging and AHY birds during incubation and early chick rearing; (2) to calculate juvenile ratios (as productivity indices) using HY counts corrected for juvenile emigration, and AHY counts at the peak of the breeding season; and (3) to compare these “corrected” ratios to traditional “concurrent” ratios and other independent measures of fecundity. I examined the assumptions and potential biases of using these methods.

Methods

Fieldwork was conducted in Desolation Sound, British Columbia (50° 06'N, 124° 47'W; Fig. 2.1). After-hatch year and hatch year Marbled Murrelets were counted in Desolation Sound and

Figure 2.1. Study area in Desolation Sound, British Columbia. Survey area is shaded in gray and the centre of the night-lighting capture area is marked with a solid circle.



the adjacent glacial fjords (Malaspina, Lancelot, Okeover and Theodosia Inlets) with at-sea surveys that followed standardized strip transect protocols (RIC 1995). At-sea surveys were replicated 24 times in 1996, 23 times in 1997 and 17 times in 1998 at average intervals of 4, 4 and 6 days respectively (range 1 – 12) between May and mid-August. Surveys were cancelled during rain or wind-wave conditions beyond 2 on the Beaufort scale. At-sea surveys ended when hatch year (HY) birds could not be accurately differentiated from after-hatch year (AHY) birds as a result of AHY birds moulting into basic (winter) plumage (Carter and Stein 1995). Surveys were estimated to cover 76% of the fledging period (Chapter 1).

Estimation of HY Movement

I defined “local survival” as the probability of a bird staying in the survey area. To estimate the daily rate of juvenile local survival, radio transmitters were attached to 16 recently fledged Marbled Murrelets captured by night-lighting (Whitworth *et al.* 1997) in the survey area from July 10 to August 10, 1998. Identification of HY birds during capture was based on plumage characteristics, egg-tooth presence, and weight (Carter and Stein 1995), although the exact age in days at first capture was unknown. Radio transmitters were ATS Model 394 (Advanced Telemetry Systems, Isanti, MN 55040 USA), weighing 2.0 g and with a battery life of 45 days. Transmitters were attached on the bird’s back, between the scapulars, using epoxy glue (Bird Adhesive, Titan Corporation, Lynnwood, WA USA) and fiberglass insect screen extensions (Titan Corporation, unpub. report). The birds were tracked during daylight from a 5.2-m Boston Whaler using a 4-element directional antenna mounted 3 m above the waterline, coupled with an ATS R4000 programmable receiver. Monitoring of the radio tagged birds was done from 7 fixed stations within the survey area, 22 times from July 11 to August 13 (every 1.5 days on average, range 1 – 4 days). Movement of juveniles out of the survey area was confirmed by sporadic boat telemetry at 3 stations outside the survey area and by aerial telemetry over a wider area using a fixed-wing Cessna 172 airplane. Aerial telemetry was done on August 10 and August 19 following the coastline from Vancouver to Desolation Sound and the northern portion of the Strait of Georgia.

The program MARK (White 1999) was used to estimate the daily local survival of radio tagged HY birds, using standard Cormack-Jolly-Seber open population models. I examined several models with different assumptions about the constancy of survival rate and recapture rate (detection) between intervals, and discriminated between models using Akaike’s Information Criterion (AIC) as described in Lebreton *et al.* (1992). I tested if survival rate (ϕ) and recapture rate (p) varied over time with likelihood ratio tests (LRT) (Cooch and White 1999) by (1) comparing the fit of the time dependent model of survival [$\phi(t) p(\cdot)$] with that of the model with

constant survival [$\phi(\cdot)p(\cdot)$], and (2) comparing the fit of the model with time dependent recapture [$\phi(\cdot)p(t)$] with that of the model with constant recapture [$\phi(\cdot)p(\cdot)$]. I used $1 - \phi$ as an estimate of the daily rate of permanent emigration. Residence time (R) was estimated as $(1/\ln(\phi))$ (White 1999). I estimated the weekly local survival rate of HY birds (ϕ^7) to allow comparison with that of AHY birds.

Correcting HY Counts

Each at-sea HY count was adjusted for juvenile turnover rate using the following correction:

$$J_n = J_o - (J_p \times \phi^d)$$

This correction estimates the number of “new” HY birds counted during a survey by calculating the number HY birds seen on the present survey that are likely to have been seen on a previous survey, and subtracting that number from the total count. J_n = the number of “new” juveniles in the observed sample from the present at-sea survey, J_o = the number of juveniles observed on the present at-sea survey, J_p = the number of juveniles observed on the previous survey, ϕ^d = the daily probability of staying in the survey area (local survival), and d = the number of days between the present survey and the previous survey. I estimated the cumulative number of HY birds for the season by adding J_n from all the surveys each year.

The estimated proportion of fledglings covered by the surveys (0.76; see Chapter 1) was used to correct the total number of HY birds of the season for early ending of the surveying period. The total number of HY birds of the season was divided by the proportion of fledglings covered by the surveys.

Estimation of AHY Movement

I estimated the weekly rate of adult local survival in the survey area. Radio transmitters were used on 40 adult Marbled Murrelets in 1998; 31 of them were captured in the survey area, and were used in the present analysis. Murrelets were captured by night-lighting from May 4 – 18. Transmitters used for adults were similar to those used for HY birds, but were attached by a subdermal anchor following the technique of Newman, et al. (in press), epoxy glue (Bird Adhesive, Titan Corporation, Lynwood, WA, USA) was used instead of a suture to secure the device. Birds were radio-tracked by boat telemetry from the first week of May to the second week of August using the same methodology as described for HY movements (above). Telemetry stations were monitored three times per day (morning, afternoon and night) during four consecutive days every 7-day period. Additional data were gathered with a Robinson 22 helicopter during aerial telemetry from May 12 - July 4. Two H-antennae were mounted on the helicopter struts, one on

each side to determine directionality, connected to a switch box and the receiver. Radios lasted an estimated 60 days, based on ad hoc observations of radios with aberrant pulse rates or tones. Three birds were removed from the analysis due to early radio malfunction (one of the birds was recaptured and the transmitter was confirmed to have failed).

Cormack-Jolly-Seber open population models were used, as described for HY birds, to estimate the weekly rate of local survival of AHY birds in the survey area. Presence and absence of radio tagged AHY birds in the survey area were aggregated into 9 1-week periods, beginning on May 8, 1998 and ending on July 10, 1998. After this period, emigration and radio malfunction would be confounded. Residence time of AHY birds was estimated as $(1/\ln(\phi))$ (White 1999). I arbitrarily defined “low” weekly adult emigration as less than 10% (greater than 90% local survival).

Juvenile Ratios

I calculated “corrected” juvenile ratios using the estimated total HY birds from at-sea surveys (corrected for turnover and proportion of the fledging period covered by surveys) divided by the mean around the AHY peak count of the season (mean AHY was calculated from surveys done from 10 days before to 10 days after the peak count each year). The rationale for using the mean number around the peak for the “corrected” juvenile ratios was that high local survival of AHY birds (see results) indicates the presence of a resident population during the breeding season. In a resident population, the fluctuation in numbers of AHY birds on the water should reflect seasonal changes in breeding chronology, therefore, the mean around the peak would better reflect the size of the local adult population. This is a minimum estimate of the local adult population because of the weekly emigration rate of adults.

I also calculated “concurrent” juvenile ratios which are a commonly used estimate obtained by dividing the number of HY birds by the number of AHY birds counted concurrently during surveys at sea conducted throughout the fledging period. I estimated the mean juvenile “concurrent” ratio for all surveys done from the first observation of a HY bird at sea to the end of the surveying period each year.

Results

HY Emigration Rate

Twelve of the 16 juveniles were detected by telemetry in the survey area on at least one occasion after capture; 9 of these were not detected in the vicinity of Desolation Sound once they left the survey area. Two other juveniles were never detected in the survey area, but were detected on one occasion each outside the survey area, 1 by boat telemetry and the other by aerial telemetry. Two

juveniles were never detected after tagging and release. Aerial telemetry detected 3 birds on August 10, 1 in the survey area and 2 outside it, and 3 on August 19 all in the general vicinity of Desolation Sound, but outside the survey area. Capture and resighting locations are shown in Figure 2.2. No juveniles with radios were detected in any other area of the Strait of Georgia.

The daily local survival rate of juveniles in the survey area (daily probability of staying, ϕ) was 0.829 ± 0.046 (95% C.I. = 0.720 – 0.902), and the recapture rate (p) was 0.718 ± 0.084 (95% C.I. = 0.528 – 0.853). The daily rate of emigration, $1 - \phi = 0.171$. The model with the best fit to the data (the one with the lowest AIC) was the model of constant survival and constant recapture rates $\phi(.)p(.)$ (Table 2.1). There was no significant variation in survival rate (model $\phi(t)p(.)$ vs. $\phi(.)p(.)$, $\chi^2 = 23.041$, $df = 19$, $P = 0.236$), or recapture rate (model $\phi(.)p(t)$ vs. $\phi(.)p(.)$, $\chi^2 = 24.242$, $df = 21$, $P = 0.282$) over time. The weekly local survival rate (ϕ^7) was 0.269 (weekly emigration rate = 0.731), and the average residence time of HY birds in the survey area was 5.3 days.

AHY Local Survival

The weekly rate of AHY local survival (ϕ) in the survey area, during the early part of the breeding season, was 0.946 ± 0.019 , with a 95% C.I. = 0.893 – 0.974 and the recapture rate was 0.771 ± 0.036 (95% C.I. = 0.694 – 0.833). The weekly rate of emigration, $1 - \phi = 0.054$. The most parsimonious model (the one with the lowest AIC) was the model with constant survival and constant recapture rates, $\phi(.)p(.)$ (Table 2.2). There was no significant variation in survival rate (model $\phi(t)p(.)$ vs. $\phi(.)p(.)$, $\chi^2 = 4.539$, $df = 7$, $P = 0.716$), or recapture rate (model $\phi(.)p(t)$ vs. $\phi(.)p(.)$, $\chi^2 = 10.455$, $df = 7$, $P = 0.164$) over the 9-week study period. The average residency time of AHY birds in the survey area was 18.01 weeks (126 days).

Correcting HY Counts

After correcting for HY dispersal, more than twice as many “new” juveniles were estimated (per survey) in 1996 (3.94 ± 1.47 , range 0 – 21, $n = 17$) than in both 1997 (1.60 ± 0.40 , range 0 – 4, $n = 13$), and 1998 (1.70 ± 0.41 , range 0 – 5, $n = 12$). For details of the raw HY counts and the correction for HY dispersal see Appendix 2.1. The cumulative total of juveniles, after correcting for turnover and proportion of fledging surveyed, was 88 in 1996, 28 in 1997, and 26 in 1998 (Table 2.3). AHY counts during at-sea surveys decreased with increasing cumulative numbers of HY counts (Fig. 2.3).

Figure 2.2. Capture and detection locations for 16 hatch year (HY) Marbled Murrelets marked with radio transmitters in Desolation Sound.

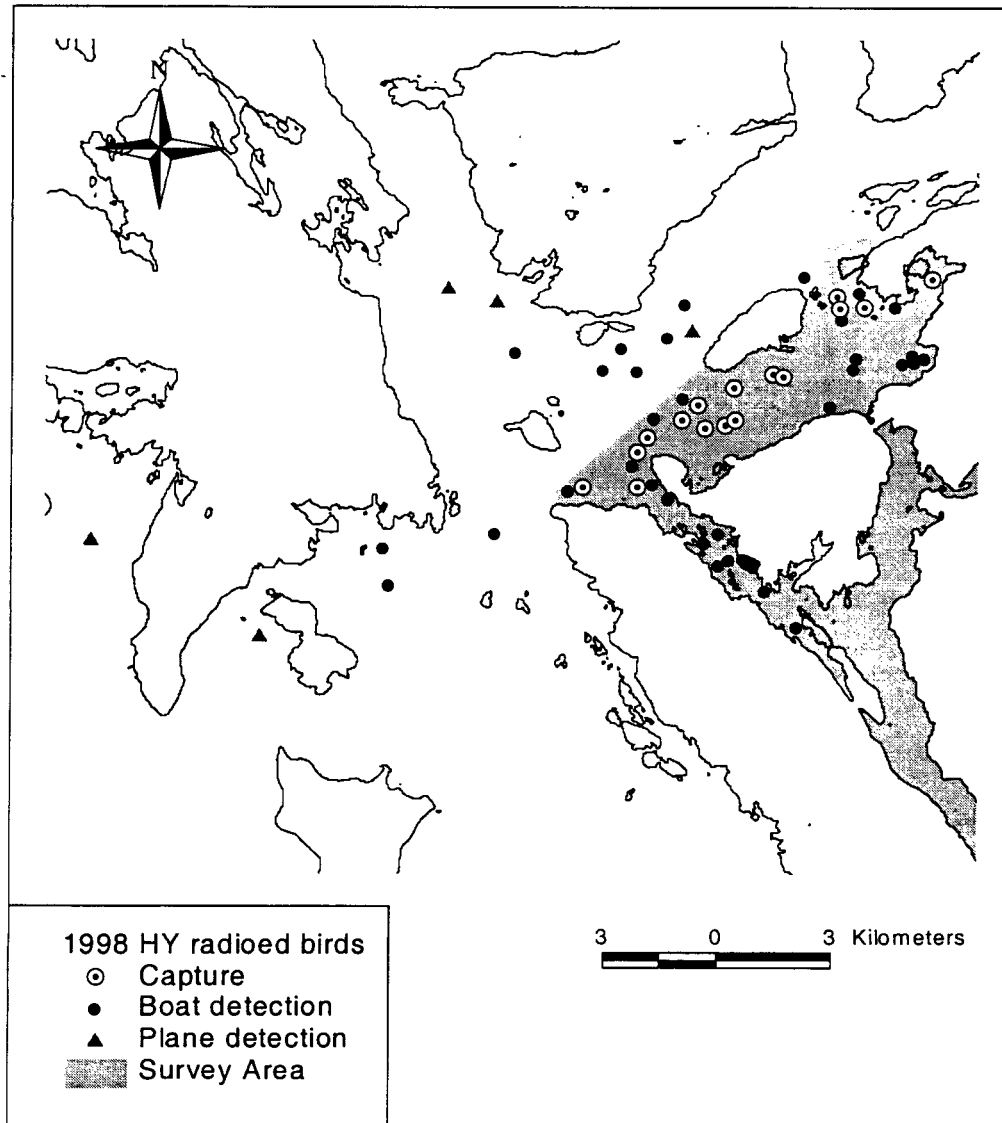


Table 2.1. Fit of survival models to HY detection data. The most parsimonious model (with the lowest AIC) is the reduced model with constant survival and recapture rates, $\phi(\cdot) p(\cdot)$.

Model	AIC	Δ AIC	No. Parameters	Model Deviance
$\phi(\cdot) p(\cdot)$	92.71	0.00	2	77.33
$\phi(t) p(\cdot)$	147.55	54.85	21	54.29
$\phi(\cdot) p(t)$	162.75	70.04	23	53.09
$\phi(t) p(t)$	616.14	523.44	38	35.05

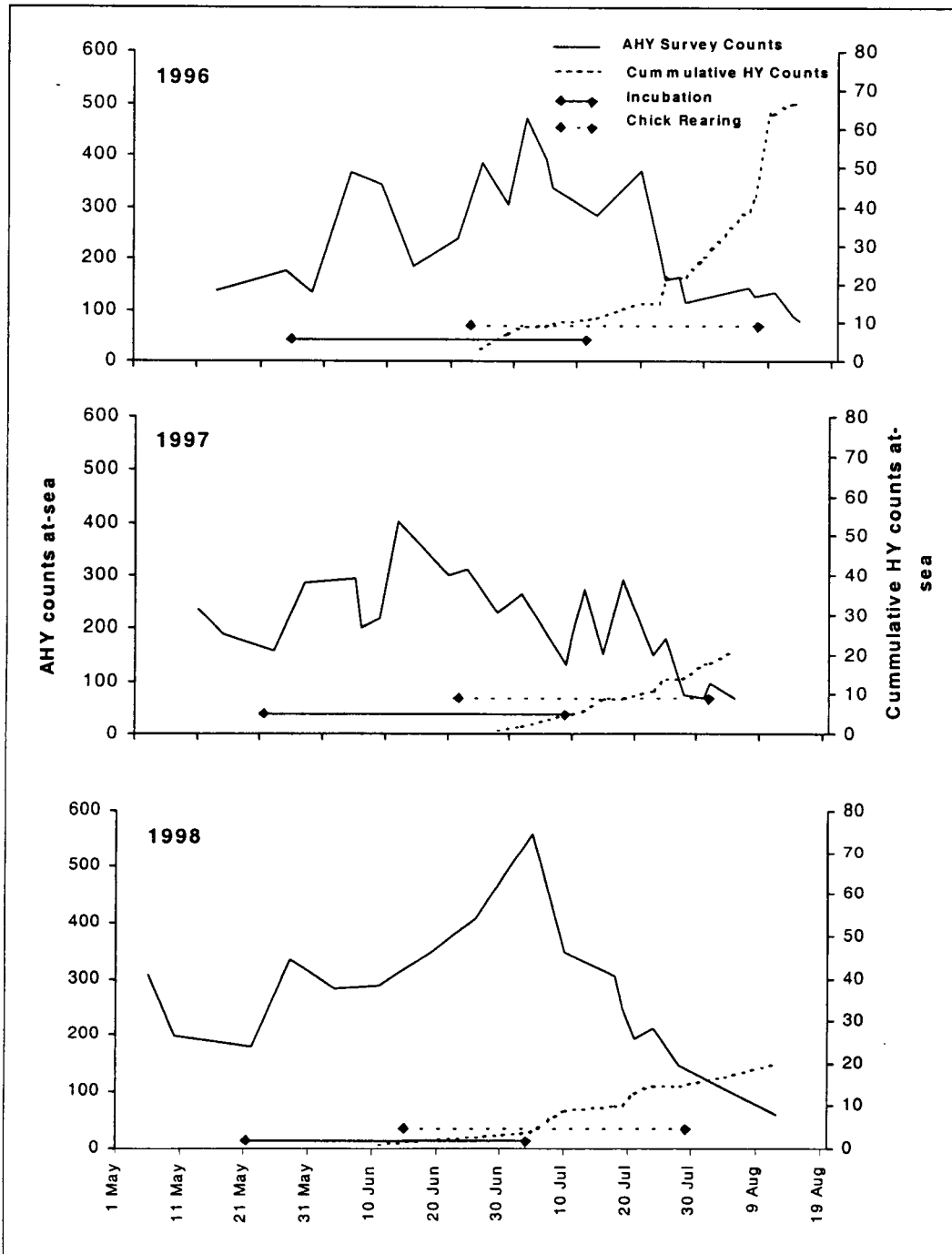
Table 2.2. Fit of basic survival models early season AHY detection data. The most parsimonious model (with the lowest AIC) is the model with constant survival and recapture rates, $\phi(\cdot) p(\cdot)$.

Model	AIC	Δ AIC	No. Parameters	Model Deviance
$\phi(\cdot) p(\cdot)$	241.94	0.00	2	105.41
$\phi(\cdot) p(t)$	246.70	4.77	9	94.95
$\phi(t) p(\cdot)$	252.62	10.68	9	100.87
$\phi(t) p(t)$	257.66	15.73	15	91.58

Table 2.3. Juvenile ratios calculated using the mean AHY bird counts from 10 days before to 10 days after the peak count of the season, and HY bird counts adjusted for turnover and proportion of fledging missed by ending surveys early.

Year	Mean Peak AHY Counts	No. Surveys (Peak Period)	No. HY Adjusted for Turnover	No. HY Adjusted for Turnover and Missed Surveys	Corrected Juvenile Ratios	Concurrent Juvenile Ratios (Mean)
1996	374	5	67	88	0.235	0.085
1997	283	5	21	28	0.099	0.027
1998	435	3	20	26	0.060	0.015
Mean ± SE	364.0 ± 44.2			43.3 ± 20.3	0.131 ± 0.053	0.042 ± 0.022

Figure 2.3. After-hatch year (AHY) and cumulative hatch year (HY) Marbled Murrelet counts during at-sea surveys. HY numbers are were corrected for juvenile turnover. Incubation and chick rearing periods are shown for each year (see Chapter 1).



Juvenile Ratios

Five surveys were done during the 20-day peak period (from 10 days before to 10 days after the peak) in 1996 (June 22– July 12), 5 in 1997 (June 2 – 22), and 3 in 1998 (June 25 – July 15). The mean “corrected” juvenile ratio for 1996 to 1998 was 0.131 ± 0.053 , ranging from 0.060 – 0.235, with a coefficient of variation of 0.699. Totals of surveys conducted from the first HY observation at sea until the end of the surveying period were: 17 in 1996 (June 25 – August 14), 14 in 1997 (June 27 – August 5), and 12 in 1998 (June 11 – August 12). The mean “concurrent” juvenile ratio was 0.042 ± 0.022 , ranging from 0.015 – 0.085 (Table 2.3).

Discussion

This study provides the first estimates of the emigration rates of HY and AHY Marbled Murrelets during the breeding season. HY birds had a high emigration rate compared to AHY birds who were residents during the breeding season. Emigration of HY birds must be accounted for prior to the calculation of the juvenile ratio, because juveniles do not accumulate in the same areas where the adults are. It appears, however, that there are other factors affecting juvenile ratios. Although AHY birds are residents, unpredictable variation in breeding success could lead to variation in at-sea counts. This may make year to year variation in juvenile ratios difficult to interpret. Although these estimates may be unique to Desolation Sound, this study highlights the importance of understanding local movements of Marbled Murrelets at sea.

Emigration of AHY birds from the survey area was low during incubation and early chick rearing (high weekly local survival, 94.6%), confirming that birds using the area of Desolation Sound during the breeding season are residents, rather than transients. The weekly 5.4% adult emigration rate is possibly related to nesting failure. It is unlikely that AHY local survival remains constant towards the end of the breeding season, given the decreases of at-sea counts which are possibly due to emigration of adults after breeding. This is one of the reasons that juvenile ratios from “concurrent” at-sea surveys could be inaccurate. Local survival of AHY birds after chick rearing was not estimated because most of the radio transmitters had either fallen off or failed by that time.

Although the weekly emigration rates of AHY birds were low, counts of birds on the water increased from incubation to chick rearing (during 1996 and 1998; see Fig. 2.3). I interpret this as nesting birds returning to the water after the hatch or failure of nests. In 1997, however, counts of birds on the water increased during incubation and decreased during chick rearing, which might have been related to extensive breeding failure early in the season. Little is known about long term variation in reproductive success of Marbled Murrelets. If the birds that failed

early emigrate out of the area before the birds that hatched chicks appear on the water, then the peak numbers during those years may not accurately estimate the number of breeders.

In contrast to that of AHY birds, HY dispersal was rapid (a weekly emigration rate of 73%). HY birds did not accumulate in the survey area. The estimated residency time for juveniles in the survey area (5.3 days) is a minimum estimate because of the unknown age of the juveniles at the time of capture. In general, most juveniles moved beyond boat or plane detection range shortly after leaving the survey area, and in some cases (7/16), they were not detected after leaving the survey area. The flight covered only a portion of the Strait of Georgia, and birds might have moved out of detection range. An adult Marbled Murrelet is known to have migrated to the San Juan Islands area in Washington State, USA (Beauchamp *et al.* 1999), and it is possible that some of the juveniles follow the same route. An influx of Marbled Murrelets occurs in the San Juan Islands starting in mid-August (M. Raphael, pers. comm.). There was no evidence of juveniles moving to nursery areas in the vicinity of Desolation Sound as reported for Alaska (Kuletz and Piatt 1999). Although there is no evidence of mortality of marked juveniles or radio loss during the study either are possible and cannot be ruled out. Radio loss would lead to an overestimate of the emigration rate, and consequently, an overestimate of the number of juveniles.

The 1996-98 average juvenile ratio (corrected for movement) was 0.13, about 3 times the ratio obtained from concurrent counts (0.042). Reported juvenile ratios from British Columbia, Washington, Oregon and California range between 0.004 and 0.041 (Beissinger 1995), are similar to the ratios estimated from "concurrent" counts. In Alaska, the reported ratios range between 0.02 and 0.11 (Kuletz and Kendall 1998), similar to the "corrected" juvenile ratios. Year to year variation in fecundity is common in alcids (Ainley and Boekelheide 1990). I also found a substantial amount of annual variation in juvenile ratio (C.V. =70%) for the three years of the study.

Despite that the average corrected juvenile ratio from Desolation Sound is higher than those reported for other areas, it is low compared to independent estimates of fecundity obtained by radio telemetry from the same population, which suggest that fecundity should be in the range of 0.16 – 0.46 (Cooke 1999). Corrected juvenile ratios were also lower than nest success in the area, estimated by tree climbing (0.33 Manley 1999), however, the two measures are not directly comparable because nest success will always be higher than fecundity. There are two possible explanations for these low juvenile ratios from at-sea surveys. The first one is an unexpectedly high proportion of non-breeding age AHY birds in the surveys counts: because both breeding age and non-breeding age AHY birds have the same plumage characteristics (Carter and Stein 1995;

Strong *et al.* 1995), non-breeding age AHY birds cannot be identified during at-sea surveys, and if the proportion of non-breeding age AHY birds in the survey area was high, juvenile ratios would be underestimated. The second explanation for low juvenile ratios is that there are differences in behaviour and distribution between AHY birds and recently fledged young. AHY birds are concentrated in and philopatric to the survey area, but juveniles are not. There is no evidence that juveniles follow their parents to the ocean (Nelson 1997); it is possible that they disperse randomly from water locations close to their nest site. Evidence from radio telemetry shows that the nests of Marbled Murrelets using in the survey area are widely distributed throughout an area much greater than the local hills and drainages (Lougheed 1999). Surveys in the Desolation Sound area, which count birds that nest over this wider area, will not count juveniles produced from the further nest sites; these surveys will only detect fledglings which have flown in from the local hills and drainages. Therefore, the HY birds counted in the survey area would be produced by a locally nesting (unknown) proportion of the total number of birds using Desolation Sound, resulting in low ratios.

Although the age structure of the murrelet population in Desolation Sound is unknown, almost all AHY birds captured in the area have a brood patch (L. Lougheed unpub. data), suggesting that only a relatively small proportion of the population are non-breeding age AHY birds (subadults). The reason that juvenile ratios are lower than other independent measures of fecundity in Desolation Sound is more likely due to differences in the distribution and behaviour of AHY and juveniles. However, because of the assumptions and possible problems in obtaining consistent estimates of AHY numbers across years, it may be that juvenile to adult ratios from at-sea surveys will not yield reliable estimates of fecundity. Accurately estimating the number of breeding age birds is essential for the calculation of representative juvenile ratios. Although these estimates are an improvement over “concurrent” ratios in that they correct for juvenile emigration, they may still be biased to an unknown extent, and long term trends could be masked. Because of these unknown biases, caution is needed when interpreting juvenile ratios from at-sea surveys.

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Appendix 2.1. Correction of HY survey counts for emigration. HY survival (ϕ) = 0.829.

Date	Juveniles Counted	No. HY birds from previous survey	No. new HY birds	Cumulative No. new HY birds
	J_o	$(J_p \times \phi^d)$	$J_n = J_o - (J_p \times \phi^d)$	
1996				
25-Jun-96	3	0	3	3
29-Jun-96	5	0	4	7
2-Jul-96	5	3	2	9
5-Jul-96	1	3	0	9
6-Jul-96	2	1	1	10
13-Jul-96	2	1	1	11
20-Jul-96	5	1	4	15
23-Jul-96	1	3	0	15
24-Jul-96	8	1	7	22
26-Jul-96	5	5	0	22
27-Jul-96	2	4	0	22
6-Aug-96	17	0	17	39
7-Aug-96	18	14	4	43
9-Aug-96	33	12	21	64
10-Aug-96	24	27	0	64
13-Aug-96	17	14	3	67
14-Aug-96	11	14	0	67
1997				
27-Jun-97	1	0	1	1
28-Jun-97	1	1	0	1
2-Jul-97	1	0	1	2
9-Jul-97	3	0	3	5
10-Jul-97	1	2	0	5
12-Jul-97	2	1	1	6
15-Jul-97	4	1	3	9
18-Jul-97	2	2	0	9
23-Jul-97	3	1	2	11
25-Jul-97	5	2	3	14
28-Jul-97	1	3	0	14
31-Jul-97	5	1	4	18
1-Aug-97	4	4	0	18
5-Aug-97	5	2	3	21
1998				
11-Jun-98	1	0	1	1
19-Jun-98	1	0	1	2
26-Jun-98	1	0	1	3
5-Jul-98	1	0	1	4
10-Jul-98	5	0	5	9
18-Jul-98	2	1	1	10
19-Jul-98	1	2	0	10
21-Jul-98	4	1	3	13
24-Jul-98	4	2	2	15
28-Jul-98	2	2	0	15
4-Aug-98	3	1	2	17
12-Aug-98	4	1	3	20

Chapter 3. At-Sea Habitat Selection by Marbled Murrelets: Changes during the Breeding Season.

Abstract. I used at-sea surveys and radio telemetry to study fine scale (< 100 km) changes in spatial and temporal distribution of Marbled Murrelets (*Brachyramphus marmoratus*) in Desolation Sound, British Columbia. Fine scale shifts in at-sea distribution and habitat selectivity have not been extensively examined for this species in relation to breeding chronology, sex or breeding status. Marbled Murrelets face unique challenges during the breeding season because of their inland nesting habits. I found that Marbled Murrelets in Desolation Sound undertake both daily and seasonal movements that appear to be related to breeding. Marbled Murrelets were, in general, more densely distributed in cooler waters (which are likely more productive, suggesting that the birds were tracking their prey). During chick rearing, however, they shifted their distribution towards waters closer to the old-growth forest. There were also diel shifts in distribution; birds moved both further from the shore and out of the inlets during the night. Both sexes showed similar patterns and changes in distribution. Although the distance from shore at night was greater for breeders than for non-breeders, they both moved further from shore during the night. Also, the proportion of breeders in the inlets was higher than that of non-breeders. I propose that these patterns of movement and distribution reflect a trade-off between the use of productive but risky waters close to the shore or the nest and safer, more distant waters.

Introduction

Habitat selection can be viewed as a scale dependent, hierarchical process, in which an animal chooses a general place to live at a large scale, and then at a fine scale, selects patches within the general area (Orians and Wittenberger 1991). At all scales, selection of a habitat by animals is thought to be based on a trade-off between the fitness benefits of resources in a certain habitat, such as availability of food, cover, and distance to breeding areas, and the costs associated with that habitat, such as exposure to predators or conspecific competitors (Fretwell 1972). The implication is that an animal should prefer a habitat in which either survival or reproductive success (or both) is enhanced, allowing it to leave more progeny than if it had selected other habitats.

If animals preferentially locate in a landscape that offers a high frequency of encounter with resources necessary for survival or reproduction (Ward and Saltz 1994), then animal density should be correlated to resource abundance, with distribution of resources influencing the movement of consumers across landscapes. Hence, the highest densities are expected in preferred habitats (O'Neil *et al.* 1988; Rosenzweig 1991). Selection of a certain habitat might be influenced by factors such as an altered balance between predation risk and food availability because of increased energetic demand during the breeding season (Cairns 1987). In this scenario, birds provisioning chicks would have to forage in areas of higher predation risk to meet energetic demands during chick rearing (including both self-provisioning and chick-provisioning).

In seabirds, at-sea density and distribution is widely regarded to be positively correlated with the distribution of their prey, especially during the breeding season when their demand for energy increases (Cairns 1987; Hunt and Schneider 1987). Oceanographic variables, such as sea-surface temperature (SST) and sea-surface salinity (SSS) are thought to reflect productivity. Cooler, more saline sea-surface waters are associated with high plankton (and planktivore) productivity due to high nutrient availability from vertical mixing in the water column, ultimately influencing the distribution and availability of prey (Hunt and Schneider 1987; Quinn and Schneider 1991; Decker *et al.* 1995; Hunt 1997). Therefore, variation in oceanographic conditions can lead to changes in seabird density, distribution and breeding success (Cairns 1987; Baird 1990; Furness 1993; Montevecchi 1993).

Marbled Murrelets (*Brachyramphus marmoratus*) spend most of their time at sea, and feed their chicks primarily on Pacific sand lance, *Ammodytes hexapterus* (Carter and Sealy 1990; Burkett 1995). Like other Alcidae (the auks), Marbled Murrelets do not carry large energy reserves relative to their rate of expenditure, consequently, they cannot forage everywhere in the ocean, but must discover areas where their prey is suitably clumped (Gaston and Jones 1998). Both sexes share the duties of incubation and chick rearing (Nelson 1997). Marbled Murrelets are unique among the auks in that they nest solitarily on the mossy branches of old-growth trees located up to 60 km inland from the ocean (Nelson 1997; Loughheed 1999; Manley 1999).

The distribution and movements of Marbled Murrelets at sea can be described at a variety of temporal and spatial scales. At a large scale (> 100 km) Marbled Murrelets are known to move from the open water to nearshore marine environments between non-breeding and breeding periods (Burger 1995). These movements to coastal areas during the breeding season have been attributed to both abundance of sand lance and accessibility to their nesting habitat (Nelson 1997). Increased concern due to the loss of murrelet nesting habitat to logging has resulted in most of the research focusing on understanding their associations with forest habitat. Consequently, fine scale (< 100 km) relationships between Marbled Murrelets and their marine habitat are poorly understood (Campbell *et al.* 1990; Nelson 1997). However, the marine habitat of the Marbled Murrelets faces pressures from coastal development, mariculture, fishing and recreational use. Understanding how Marbled Murrelets use the marine habitat is important because the availability and quality of this habitat is critical for their survival and reproductive success.

The purpose of my study was to test the hypothesis that Marbled Murrelets are not randomly distributed over the marine environment, and to investigate the daily and seasonal relationships between marine habitat and murrelet density and distribution. To do this, I measured the oceanographic variables SST and SSS, and compared these and proximity to the nesting habitat with density and distribution of Marbled Murrelets at sea during different stages of the breeding season.

Physical variables have been emphasized among those thought to determine the structure of bird assemblages, in part because they are much easier to measure than are biological ones (Wiens 1989). Relationships among oceanographic variables and murrelet density have been previously documented (Kaiser *et al.* 1991; Burger 1996), but small scale changes in spatial and temporal distribution have not been studied thoroughly in relation to breeding chronology, sex or breeding status.

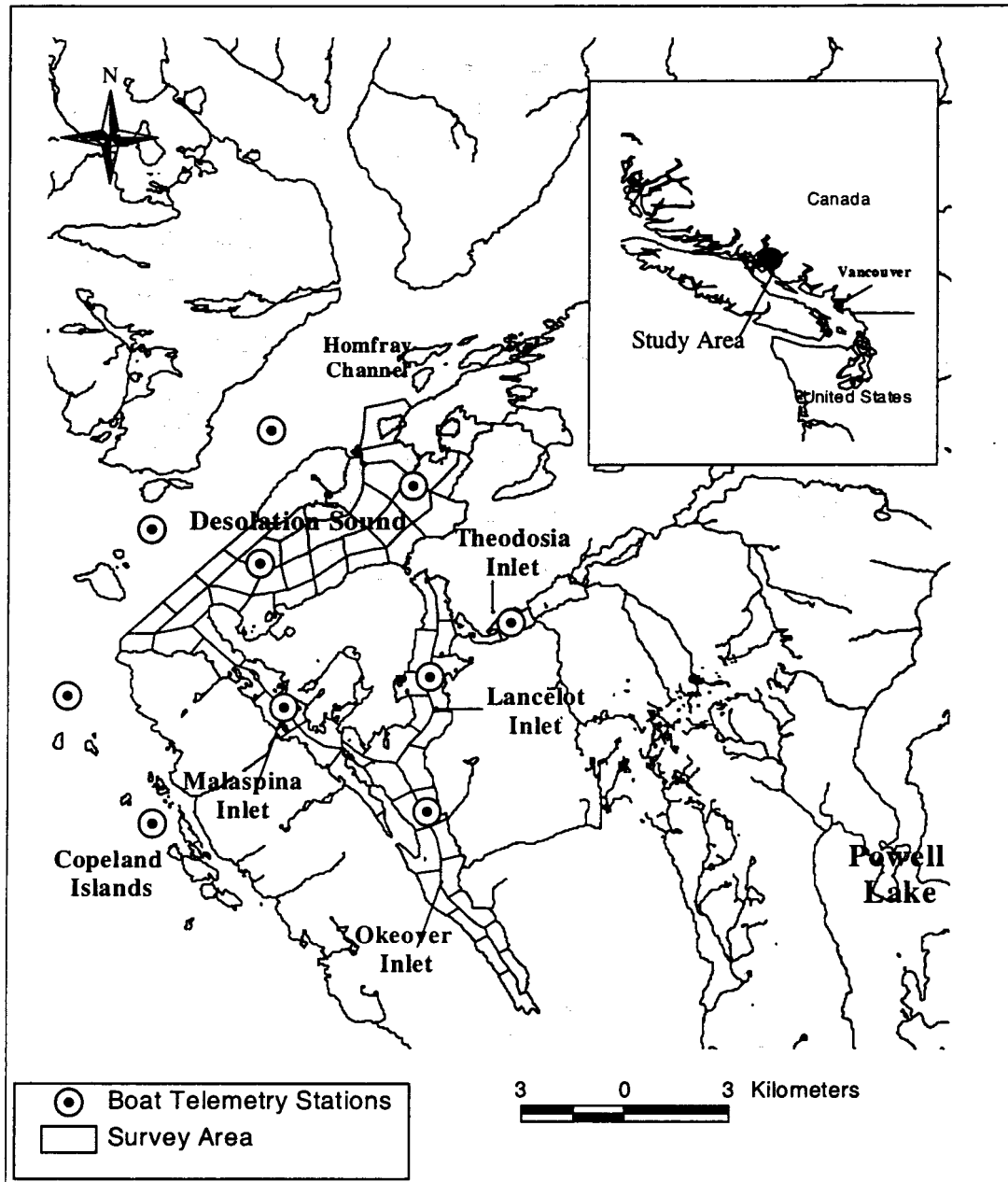
I studied radio-tagged birds of known sex and breeding status, to facilitate a more thorough understanding of their habitat choice and distribution on the water, both daily and seasonally. During the breeding season, Marbled Murrelets may adjust their local distribution to take advantage of prey concentrations, or to minimize the energetic consequences of flying between feeding and nesting areas. Throughout the day, murrelets might also move between foraging and resting sessions.

Methods

Fieldwork was conducted in Desolation Sound, British Columbia (50° 06'N, 124° 47'W; Fig. 3.1). I conducted at-sea surveys to study the relationships among murrelet densities (Marbled Murrelets / km²) and habitat variables or breeding chronology periods. These surveys were conducted regularly between May and mid-August from 1996 – 1998. The survey area included Desolation Sound and the adjacent glacial fjords of Malaspina, Lancelot, Okeover and Theodosia Inlets (between 50° 04'N, 124° 50'W and 50° 07'N, 124° 44'W, Fig. 3.1). The total survey area was 50.17 km² (24.33 and 25.84 km² for inlets and Sound, respectively) divided into 71 polygons averaging 0.71 km² each (range 0.23 - 1.29 km²) (Fig. 3.1). Following standardized transects (RIC 1995) that went through all the polygons, observers recorded the presence and plumage of all Marbled Murrelets encountered along the route. Surveys were cancelled during rain or wind-wave conditions beyond 2 on the Beaufort scale. Sea-surface temperature (SST) and sea-surface salinity (SSS) were measured at each polygon with a YSI Model 33 S-C-T Meter (Yellow Springs Instrument Co., Inc., Yellow Springs, OH 45387 USA). Totals of 24, 23 and 17 surveys were completed during the 1996, 1997 and 1998 breeding seasons, with an average time between surveys of 4, 4 and 6 days, respectively (range 1 - 12 days). Tests for effects of chronology periods (incubation and chick rearing) on murrelet density included only surveys done during the “core incubation” and “core chick rearing” periods. Core periods correspond to the middle 50% incubation or chick rearing events, estimated for Desolation Sound for the three years of the study (see Chapter 1).

In 1998, I used individually marked birds of known sex and breeding status to study diel and seasonal patterns of habitat use and distribution. Radio transmitters were deployed on a sample of 40 Marbled Murrelets captured by night-lighting (modified from Whitworth *et al.* 1997) from May 4 to

Figure 3.1. Study area in Desolation Sound, British Columbia, showing the survey area (including polygon boundaries) and boat telemetry monitoring stations. Marbled Murrelets were counted in the survey area during the breeding seasons of 1996, 1997 and 1998.



May 18 in Desolation Sound. A small blood sample was collected from each bird to determine sex, through analysis of DNA (Griffiths *et al.* 1996). Transmitters were attached using a sub-dermal anchor modified from a technique of Newman *et al.* (in press), but epoxy glue (Bird Adhesive, Titan Corporation, USA) was used instead of a suture to secure the device. Radio transmitters were ATS Model 394 (Advanced Telemetry Systems, Isanti, MN 55040 USA), weighing 2.0 g and with a battery life of 45 days. Birds were radio-tracked every day, weather permitting, by boat, helicopter or both. Boat telemetry was done from the first week of May to the second week of August from a 5.2-m Boston Whaler using a 4-element directional antenna mounted 3 m above the waterline, coupled with an ATS R4000 programmable receiver. Ten telemetry stations (Fig. 3.1) were monitored during the day and during the night, for 4 consecutive days every seven-day period. Additional daytime data were gathered by aerial telemetry which was done daily, weather permitting, from May 12 - July 4 using a Robinson 22 helicopter. Two H-antennae were mounted on the helicopter struts, one on each side to determine direction, connected to a switch box and then to the receiver. Signal strength (in the range of 1- 5) was recorded for all detections.

Independence between successive observations is an implicit assumption in most spatial analysis of animal movements (Swihart and Slade 1985; Aebischer *et al.* 1993). To avoid problems due to autocorrelation between observations, I used only one diurnal and one nocturnal location per day for each bird. Day (DY) detections went from 0500 - 2059 hours, and night (NT) detections went from 2100 - 0459 hours. The location used for each period (DY or NT) was the one with the highest signal strength.

Marbled Murrelets have 24-hour incubation shifts, with one adult incubating while the other forages at sea (Simons 1980; Hirsch *et al.* 1981; Nelson and Peck 1995). This results in a characteristic daily “on-off” (on and off the nest) pattern at sea during the incubation period. The daily on-off patterns of radioed birds were tracked on the water to detect changes in breeding status. Nest initiation was defined as the date when a breeding bird equipped with a radio transmitter started to show an on-off pattern on the water, and the start of chick rearing was when this on-off pattern stopped. Nests were monitored during the chick rearing period to confirm that the nest was active. Breeding stage (pre-breeding, incubation, chick rearing or failed) was assigned to all detections based on nest initiation date.

Factors Affecting Distribution at Sea

I examined the relationships among breeding stage, distance to the forest (DFOR) or ocean productivity (indirectly measured by SST and SSS) and changes in distribution of Marbled Murrelets within the survey area. DFOR was measured as the straight line distance from the centre of the polygon to the closest patch of old-growth forest (> 20 ha) using ArcView GIS (Environmental

Systems Research Institute, Inc.). I tested for interannual variation in each SST and SSS using one-way Analysis of Variance (ANOVA). Murrelet density for each polygon (murrelets / polygon area) was summarized by chronology stage (incubation and chick rearing) and tested for year to year and within year differences with two-way ANOVA. Pairwise comparisons were done with a post-hoc Student-Newman-Keuls test (SNK). Density of murrelets in polygons was \log_{10} transformed to allow parametric tests (Sokal and Rohlf 1981). The relative importance of the various habitat characteristics in explaining the variance in murrelet density was assessed by multiple regression with backward elimination (Significance Level to Stay, $SLS = 0.1$), by chronology stage. The variance inflation factor (Vif) was estimated for all independent variables. Multicollinearity is assumed not to be significant when the variance inflation due to correlated variables is less than 10 (Stevens 1992). I studied the changes in the relationships between murrelet density and explanatory habitat variables (DFOR and SST), selected by multiple regression, throughout the breeding season by regressing estimates of the slope of the regression (β) of DFOR or SST versus density from each survey against date. Linear relationships and year class differences in β (with date) were investigated with analyses of covariance (ANCOVA). Year differences were assessed by calculating a T value for the null hypothesis of equality of all pairs of adjusted means (SAS Institute 1991). If year class differences were found, each year was analysed separately. I examined the change in the magnitude and direction of the relationship among β 's of density and habitat characteristics for first and higher order (polynomial) relationships with ordinary least squares linear regression.

Habitat Selectivity

Seasonal and yearly changes in Marbled Murrelet selectivity for habitat characteristics were determined using Bonferroni's inequality as advocated by Haney and Solow (1992). I studied selectivity for four different categories of SST and DFOR, which were the explanatory variables selected using multiple regression (above). The limits of the four categories were defined by quantiles (the 25th, 50th and 75th percentiles) calculated with PROC UNIVARIATE (SAS), and based on all available habitat in all years. Differences in observed and expected proportional use (use and availability) of these habitat categories were assessed for significance by examining the confidence interval. The 95% confidence intervals were calculated around the observed proportion of use, and then the interval was compared to availability (the expected proportion). Categories with confidence intervals falling outside availability were considered significantly over or under used.

Diel Shifts in Distribution: Effects of Sex and Breeding Status

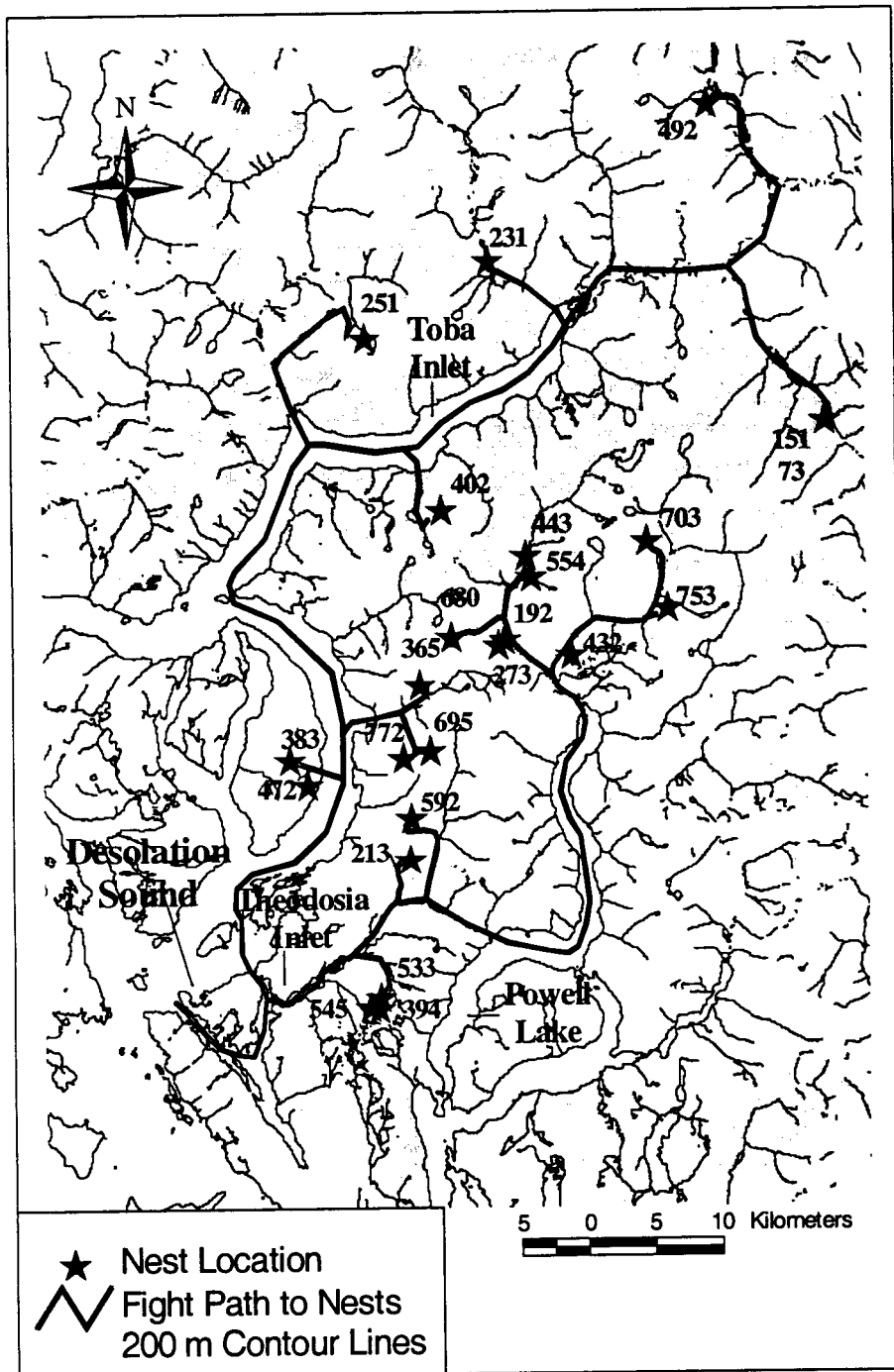
I investigated diel shifts in distribution using individuals marked with radio transmitters. First, I studied the relationship between distance to the shore and murrelet diurnal and nocturnal distribution.

Because Theodosia, Lancelot, Okeover and Malaspina Inlets are narrower than the Sound, forming a relatively enclosed area surrounded by shore (Fig. 3.1), I then compare the proportional use of the inlets between day (DY) and night (NT). If murrelets are avoiding areas close to shore at night, the inlets should be also avoided. Aerial telemetry detections were not included in these analyses because that method was only in use during the day. Diel changes in distance to shore were examined by comparing the average distance to the closest shoreline from “paired” DY and NT water locations. I defined a DY-NT pair as two consecutive observations at each period (DY and NT), that is, a NT detection paired with a detection from either the previous DY or the following DY period. Diel changes in inlet use were examined by calculating the proportion of detections in the inlets for each DY and NT period from the total DY or NT detections, respectively. Only birds with 2 or more detections in the inlets were included in this analysis. Differences between males and females and breeders and non-breeders (for both distance to shore and use if inlets) were tested using general linear models with time of day (DY or NT) as a repeated measure. The dependent variable “distance to shore” was square root transformed to normalize the data. Standard transformations were not effective in normalizing the proportions of DY and NT inlet use, so to allow the use of parametric tests, the proportions were ranked prior to analysis (Seaman *et al.* 1994).

At-sea Movement between Breeding Stages

I tested the hypothesis that breeding Marbled Murrelets move closer to the nest site with changes in breeding stage (pre-breeding, incubation and chick rearing). I used water locations from breeding birds marked with radio transmitters with at least 5 locations during at least 2 of the breeding periods. The harmonic mean of the water locations at each stage was used to estimate the centre of activity. Harmonic means are useful to determine foraging or roosting areas because they reflects the location of highest frequency of use (Dixon and Chapman 1980; White and Garrott 1990). Harmonic means were calculated using the animal movement extension (Hooge and Eichenlaub 1999) in ArcView, with a grid size of 10. I restricted the analysis to DY water locations because the majority of chick feeding occurs from dawn to dusk (Nelson and Hamer 1995; Nelson 1997; Manley 1999), therefore water locations during the day should better reflect foraging areas. I measured the distance from the centre of activity to the nest site at the different breeding stages using the inferred flight paths (Fig. 3.2) with ArcView. Marbled Murrelets usually fly up creeks and through other gaps in the canopy (Nelson and Peck 1995; Manley 1999). Flight paths were inferred both from observations of flying birds and from detections of radio tagged birds from ground-based radio telemetry (L. Loughheed,

Figure 3.2. Nest of Marbled Murrelets located by radio telemetry in 1998 and flight paths from nests to foraging areas inferred both from observations of flying birds and detections of radio tagged birds from ground-based radio telemetry. The distances traveled by radioed birds from the nest to their centres of activity at different stages of the breeding period were measured following these flight paths.



unpub. data). In 1998, 11 monitoring stations were set up in all major drainages, usually near active nests of radio tagged birds. During chick rearing, visual and radio telemetry surveys were done at these stations twice a day, from an hour before until an hour after both dawn and dusk, for at least 3 consecutive days. Telemetry monitoring was also done throughout the day on most occasions.

I compared the distance traveled from the nest site to foraging areas (activity centres) between pre-breeding and incubation and between incubation and chick rearing. My prediction was that murrelets should move closer to the nest site when the energy demand of the nestling is the highest, to minimize the cost of provisioning the nestling (Kuletz *et al.* 1995). I used one-tailed paired t-tests to compare mean distances to the nest site for the two sets of periods: pre-breeding and incubation, and incubation and chick rearing.

Seasonal Differences in the Use of Inlets and Sound

I tested for effects of location (inlets or Sound) and breeding chronology on density of Marbled Murrelets at sea during 1996, 1997 and 1998. Counts of Marbled Murrelets from at-sea surveys were used to calculate the densities for each location (inlet and Sound). I first tested for a year effect on density of Marbled Murrelets using one-way ANOVA. Differences between incubation and chick rearing were tested using two-way ANOVA. A square root transformation on the density variable was used to allow normality tests (Sokal and Rohlf 1981).

Unless otherwise indicated, statistical tests were two tailed, and statistical significance was accepted at $P \leq 0.05$. All statistical analyses were done using SAS (SAS Institute 1991).

Results

Factors Affecting Distribution at Sea

Murrelet density by polygon did not vary among years or with breeding chronology ($F_{2, 420} = 2.53$, $P = 0.080$; $F_{2, 420} = 0.99$, $P = 0.321$), however, there were significant variations among years in SST and SSS ($F_{2, 210} = 11.44$, $P < 0.001$; $F_{2, 210} = 130.09$, $P < 0.001$). Student-Newman-Keuls' multiple range tests showed that SST was significantly cooler in 1996 compared to 1997 and 1998. There were no differences in SST between 1997 and 1998. SSS in 1997 was significantly lower than in 1996 and 1998, with no significant differences between 1996 and 1998 (Fig. 3.3).

The summary of the multiple regression (with backwards elimination) of habitat variables on murrelet density is shown in Table 3.1. During the breeding seasons of 1997 and 1998, murrelet densities were always negatively correlated with SST, or in other words, higher murrelet densities were found in cooler waters. During chick rearing in 1997 and during both breeding stages (incubation and chick rearing) in 1998, DFOR was also a significant explanatory variable for murrelet density. DFOR was negatively correlated to murrelet density in the survey area. In 1996, the overall

Figure 3.3. Mean sea-surface temperature (SST) and sea-surface salinity (SSS, ppt) by year. SST was significantly cooler 1996 than in 1997 and 1998. There were no differences in SST between 1997 and 1998. In 1997, SSS was significantly lower than in 1996 and 1998, with no significant differences between 1996 and 1998. INC = incubation, and CR = chick rearing.

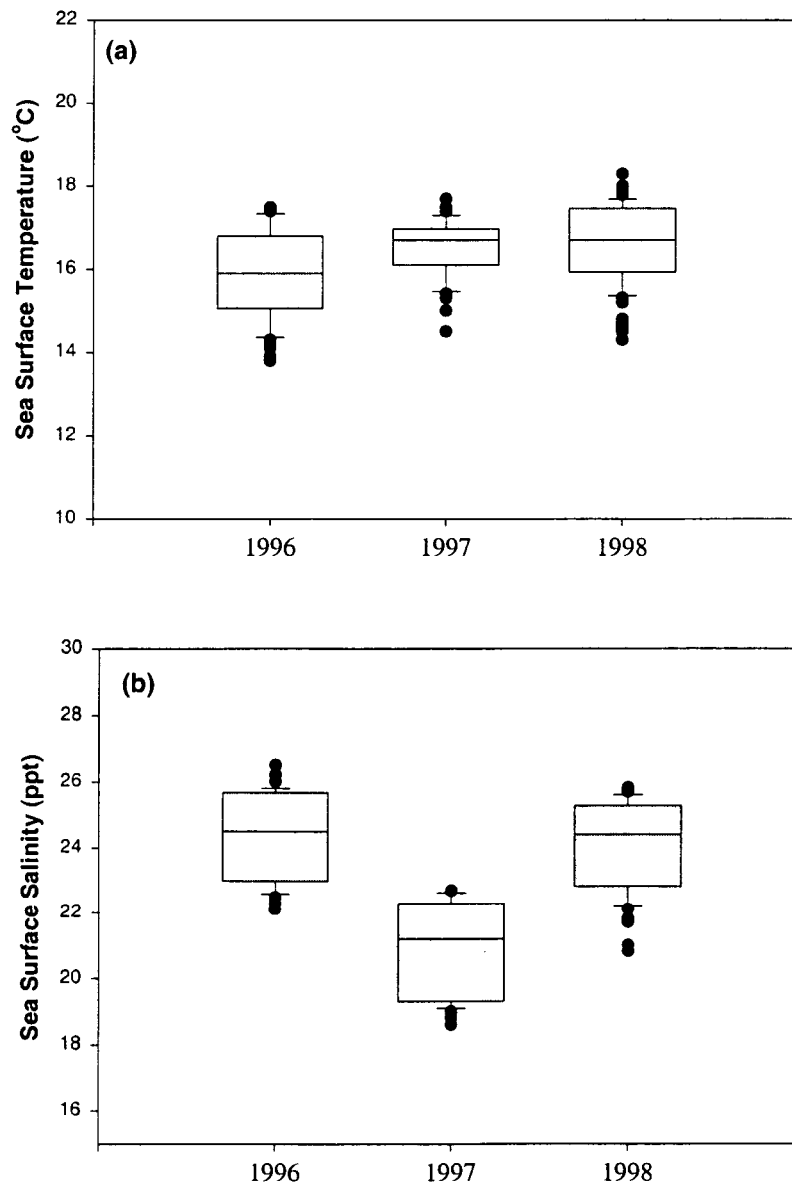


Table 3.1. Summary of variable selection (with backwards elimination, $SLS=0.1$) and the statistics from multiple regressions of habitat variables on Marbled Murrelet density at sea. Habitat variables (distance to the forest (DFOR), sea-surface temperature (SST), sea-surface salinity (SSS)), and R^2 are shown by year and by breeding stage.

Breeding		All Season			Incubation				Chick Rearing			
Season												
Stage												
Year	Var	β	P	Model R^2	Var	β	P	Model R^2	Var	β	P	Model R^2
1996	SST	-0.194	0.022	0.077	NONE				NONE			
	SSS	-0.133	0.036									
1997	DFOR	-0.040	0.043	0.134	SST	-0.221	0.014	0.084	DFOR	-0.110	<0.001	0.342
	SST	-0.177	0.022									
1998	DFOR	-0.052	0.005	0.336	DFOR	-0.077	0.004	0.273	DFOR	-0.165	<0.001	0.527
	SST	-0.208	< 0.001									

murrelet density was related to the season average of SST and SSS, but all explanatory habitat variables were eliminated during the selection process for the incubation and chick rearing periods. Regressions murrelet density on DFOR, SST and SSS by breeding periods and by year are shown in Figure 3.4.

The slopes of the relationship (β) between DFOR and murrelet density (by survey) did not vary across years ($F_{2,57} = 2.69, P = 0.076$) but did vary within the year ($F_{1,57} = 28.13, P < 0.001$). The slopes of the relationship (β) between SST and murrelet density (by survey) varied both across years ($F_{2,57} = 3.81, P = 0.028$) and within the year ($F_{1,57} = 46.64, P < 0.001$). There was a shift in habitat selectivity during the breeding season with preference for areas closer to the forest and preference for cooler temperature waters becoming stronger as the season progressed (especially during chick rearing) but these eased towards the end of the breeding season (Fig. 3.5). A polynomial equation fit estimates of Beta regressed onto date (the higher order relationship was significant) for DFOR (Least squares linear regression, $\beta_{(\text{DFOR vs. density})} = -0.026(\text{date}) + 0.00007(\text{date})^2 + 2.433, F_{2,60} = 34.46, P < 0.001$, Fig 3.5a). Since the relationships (β) of SST and murrelet density (by survey) varied between years ($T=2.67, P<0.01$) each year was assessed separately. In 1996, there was a simple linear decrease in β with time (Least squares linear regression, $\beta_{(\text{SST vs. density})} = -0.023(\text{date}) + 2.313, F_{2,20} = 5.83, P < 0.010$, Fig. 3.5b). For both 1997 and 1998, a polynomial equation fit the estimates of β with date, indicating that the relationship was curvilinear ((Least squares linear regression, 1997: $\beta_{(\text{SST vs. density})} = -0.064(\text{date}) + 0.0002(\text{date})^2 + 6.100, F_{2,20} = 18.89, P < 0.001$, Fig. 3.5c, 1998: $\beta_{(\text{SST vs. density})} = -0.035(\text{date}) + 0.0001(\text{date})^2 + 3.330, F_{2,14} = 14.31, P < 0.001$, Fig. 3.5d).

Habitat Selectivity

The coldest water available was preferred on most years during incubation and chick rearing, and the warmest waters were usually avoided (Table 3.2). Overall, areas of water temperatures greater than 17 °C were avoided. Temperatures from 13.5 – 15.7 were preferred, and if these were not available, temperatures under 17°C were chosen. Average densities and SST during incubation and chick rearing for 1996 – 1998 are shown in Figures 3.6 – 3.8, respectively.

Preference for distances close to or away from the forest depended on breeding stage. Murrelets used areas further from old-growth forest during incubation and areas close to forest during chick rearing, except during incubation of 1998 and chick rearing of 1996 when all DFOR categories were used in proportion to availability (Table 3.3). Areas further away from the forest (> 9.9 km) were used in significantly lower proportion than expected during chick rearing but significantly more

Figure 3.4. Habitat measures and density of Marbled Murrelets by year and breeding stage. Sea-surface temperature (SST) and distance to the old-growth forest (DFOR) were significant explanatory variables of murrelet density in 1997 and 1998. The regression lines are shown for the significant variables (selected with backwards elimination). INC = incubation, and CR = chick rearing.

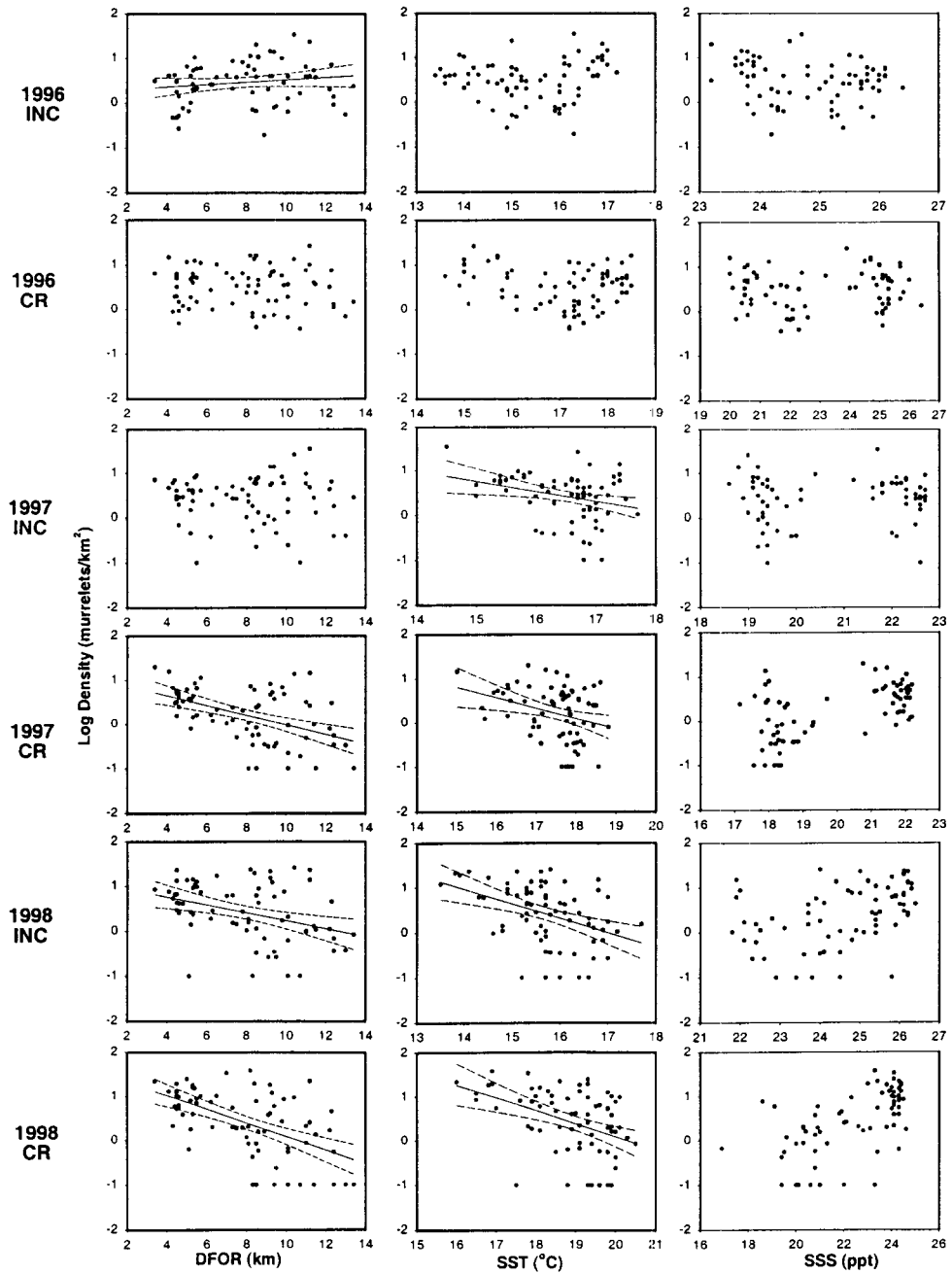


Figure 3.5. Changes to β (the slope of the regression of habitat variable vs. density of Marbled Murrelets, by survey) over the breeding season (1996 – 1998). $\beta_{(habitat\ variable\ vs.\ murrelet\ density)}$ gradually becomes negative for both SST and DFOR during breeding, indicating that birds are progressively shifting to colder waters and closer to old-growth forest as the breeding season progresses. $\beta_{(DFOR\ vs.\ murrelet\ density)}$ was similar among years, so data were pooled (a); a polynomial equation fit the estimates over time. $\beta_{(SST\ vs.\ murrelet\ density)}$ for 1996 (b) was different than for 1997 (c) and 1998 (d). In 1996 the relationship between β and time was linear, but in 1997 and 1998 polynomial equations fit the estimates with time. MAMU= Marbled Murrelet.

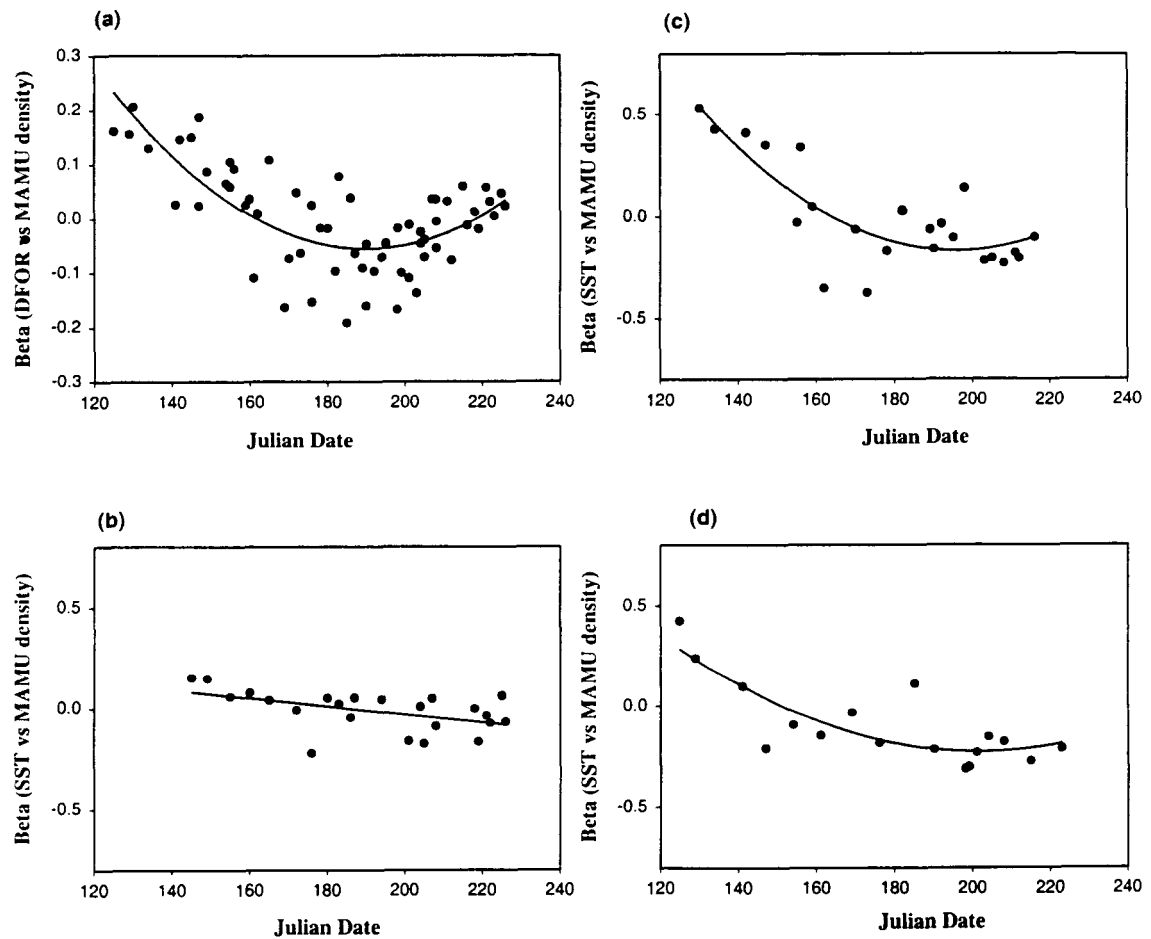


Table 3.2. Differential use of area by chronological stage and category of sea-surface temperature. The coldest water categories tended to be used more than would be expected if distribution was random. Note that in 1996 the warmest water category was not available during incubation, while in 1998 (an El Niño year) the coldest water category was not available during chick rearing. INC = Incubation, CR = Chick rearing, Under = significantly lower density than expected, Over = significantly higher density than expected, - = expected density if habitat choice was random with respect to SST, N/A = not available.

Nesting Chronology	Year	SST < 15.7°C	15.7°C ≤ SST < 16.5°C	16.5°C ≤ SST < 17°C	SST ≥ 17°C
INC	1996	Under	-	Over	-
INC	1997	Over	-	-	-
INC	1998	Over	-	Under	Under
CR	1996	Over	-	Under	Under
CR	1997	Over	-	Over	Under
CR	1998	N/A	Over	Over	Under

Figure 3.6. Average density of Marbled Murrelets at-sea (murrelets / km²), based upon boat surveys, during incubation and chick rearing in relation to sea-surface temperature in 1996.

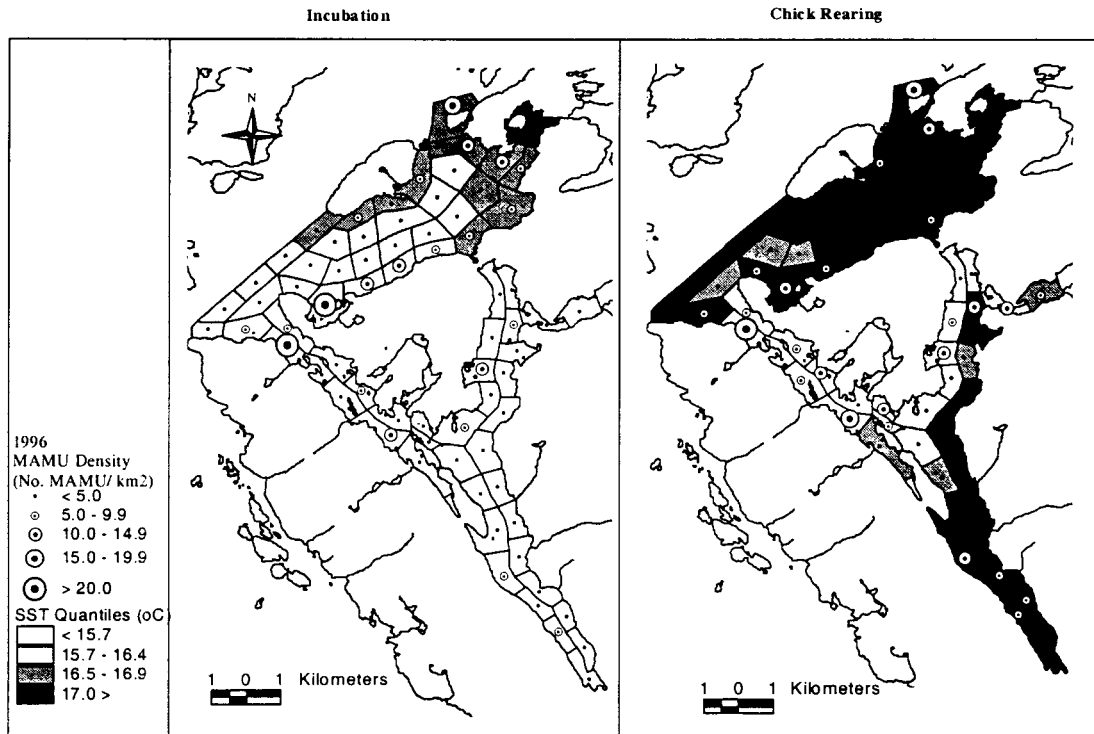


Figure 3.7. Average density of Marbled Murrelets at-sea (murrelets / km²), based upon boat surveys, during incubation and chick rearing, based upon boat surveys, in relation to sea-surface temperature in 1997.

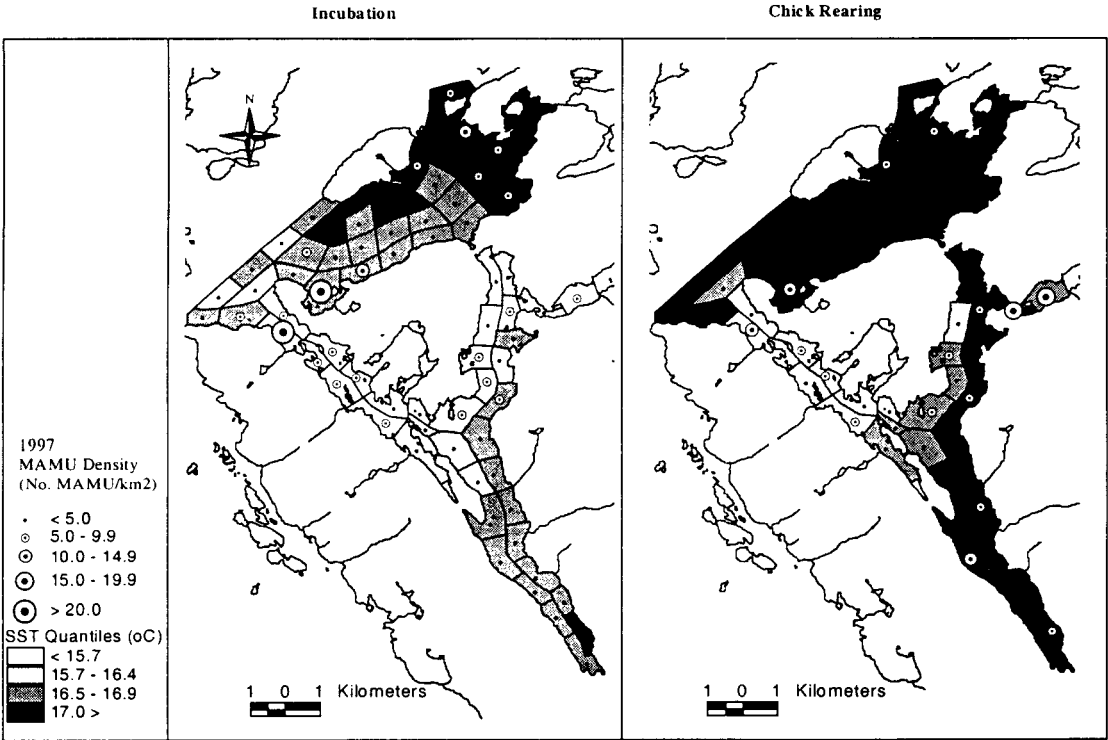


Figure 3.8. Average density of Marbled Murrelets at-sea (murrelets / km²), based upon boat surveys, during incubation and chick rearing in relation to sea-surface temperature in 1998.

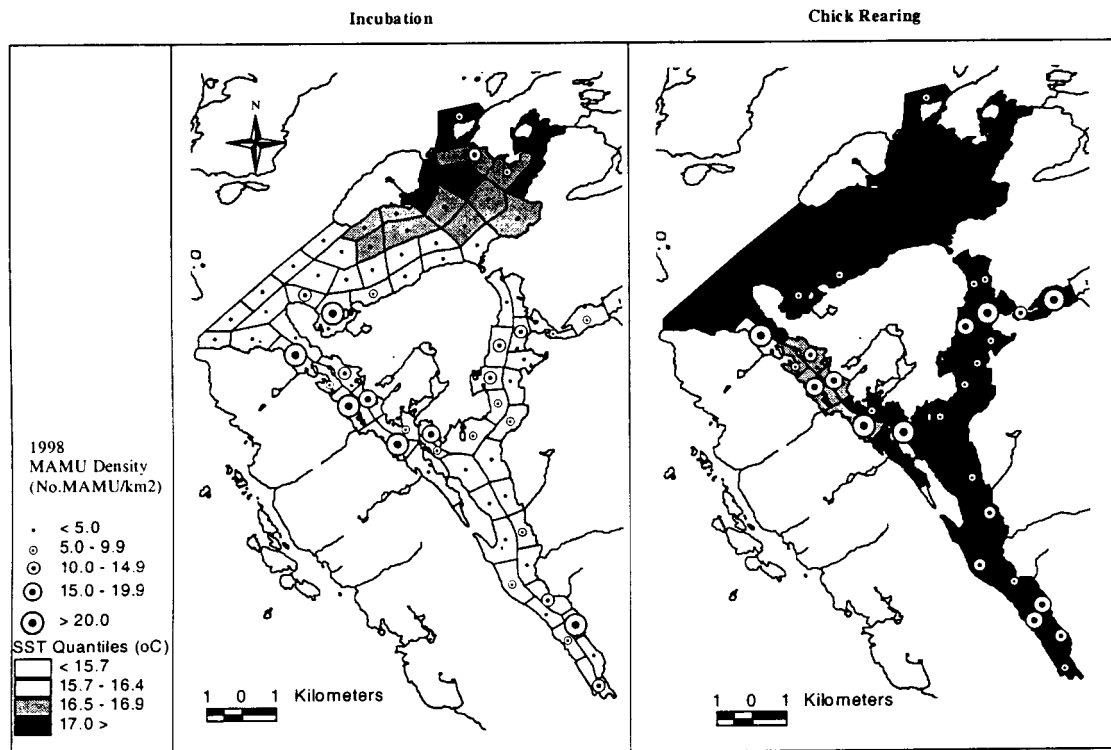


Table 3.3. Differential use of area by chronological stage and distance to the nearest old-growth forest (DFOR). During incubation, Marbled Murrelets tended to be in polygons furthest from the forest. When rearing chicks, murrelets preferred the closest polygons. INC = Incubation, CR = Chick rearing, Under = significantly lower density than expected, Over = significantly higher density than expected, - = expected density if habitat choice was random with respect to DFOR.

Nesting Chronology	Year	DFOR < 5.3 km	5.3 km < DFOR < 8.2 km	8.2 km < DFOR < 9.9 km	DFOR > 9.9 km
INC	1996	Under	-	-	Over
INC	1997	Under	-	-	Over
INC	1998	-	-	-	-
CR	1996	-	-	-	-
CR	1997	Over	-	Under	-
CR	1998	Over	Over	Under	Under

than expected during incubation. Distance to old-growth forest and average densities during incubation and chick rearing for 1996, 1997 and 1998 are shown in Figures 3.9 – 3.11, respectively. Also, a summary of the computations for SST and DFOR, are presented in Appendixes 3.1 and 3.2, respectively.

Diel Shifts in Distribution: Effects of Sex and Breeding Status

There were significant differences between distance to shore during the day and during the night ($F_{1, 36} = 37.28, P < 0.001$), with birds moving away from shore at night and closer to shore during the day. The mean difference between distance to shore during day and night was 0.18 ± 0.02 km. There were no differences between males and females ($F_{1, 34} = 0.04, P = 0.846$). Although, breeders moved further from shore than non-breeders ($F_{1, 35} = 4.83, P = 0.035$), both breeders and non-breeders moved significantly further from shore during the night ($F_{1, 40} = 23.38, P < 0.001$; $F_{1, 30} = 16.58, P < 0.001$, respectively). The average distances from shore for day and night locations are listed in Appendix 3.3. I found the same pattern of avoidance for nearshore areas when comparing the proportional use of the inlets during DY or NT; inlets were avoided during the night by Marbled Murrelets, regardless of sex or breeding status. The mean proportion of detections in the inlets during the day was significantly higher than the mean proportion of detections during the night ($F_{1, 20} = 33.86, P < 0.001$, Fig. 3.12). Sex did not have an effect on inlet use ($F_{1, 19} = 0.00, P = 0.95$), but there were differences in inlet use between breeders and non-breeders ($F_{1, 19} = 4.55, P = 0.046$), with breeders using the inlets at a higher proportion than non breeders.

At-sea Movement between Breeding Stages

The mean difference in distance to the nest site from activity centres between pre-breeding and incubation was 2.14 ± 1.64 km, but this was not significantly different from zero ($t_{6,1}=1.31, P=0.125$, Fig. 3.13). The mean difference in distance to the nest site from activity centres between incubation and chick rearing was 8.67 ± 4.42 km, which was greater than a zero difference ($t_{8,1}=1.96, P=0.045$, Fig. 3.14); birds moved closer to the nesting areas during chick rearing.

Seasonal Differences in Use of Inlets and Sound

Mean density of murrelets did not change amongst years ($F_{2, 105} = 1.33, P = 0.269$), therefore, the effects of location and chronology on density were tested using the pooled data from all years. Breeding chronology period did not have an effect on density ($F_{1, 105} = 3.04, P = 0.085$), but there were significant interactions between location (inlets and Sound) and chronology ($F_{1, 105} = 25.98, P < 0.001$). The intensity of use of the Sound and the inlets changed with breeding chronology. Marbled Murrelet density was higher in the Sound during incubation, but it was higher in the inlets during chick rearing (Fig. 3.15).

Figure 3.9. Average density of Marbled Murrelets at-sea (murrelets / km²), based upon boat surveys, during incubation and chick rearing in relation to distance to the forest in 1996.

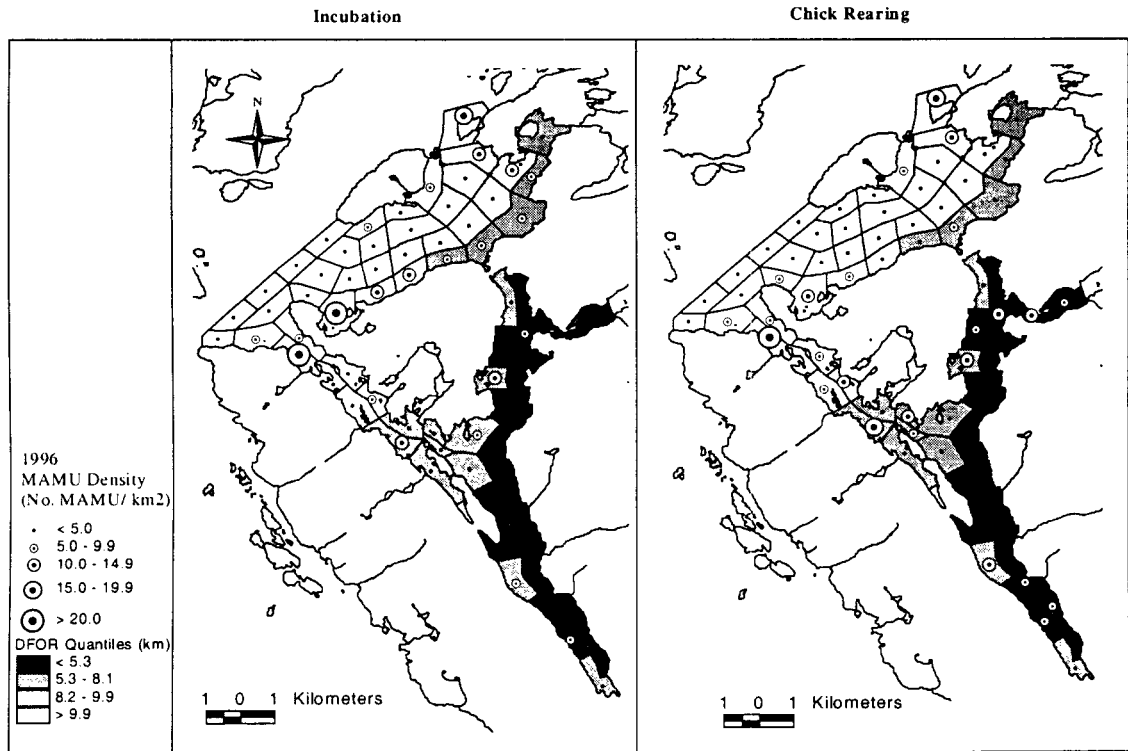


Figure 3.10. Average density of Marbled Murrelets at-sea (murrelets / km²), based upon boat surveys, during incubation and chick rearing in relation to distance to the forest in 1997.

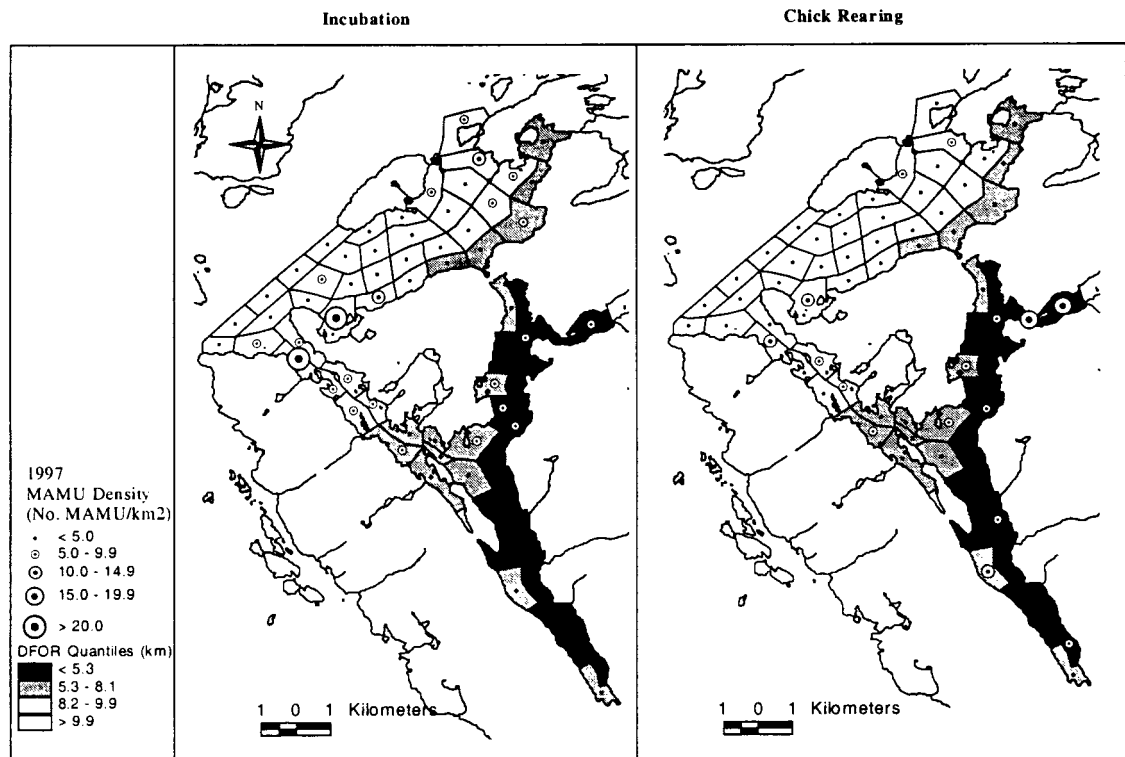


Figure 3.11. Average density of Marbled Murrelets at-sea (murrelets / km²), based upon boat surveys, during incubation and chick rearing in relation to distance to the forest in 1998.

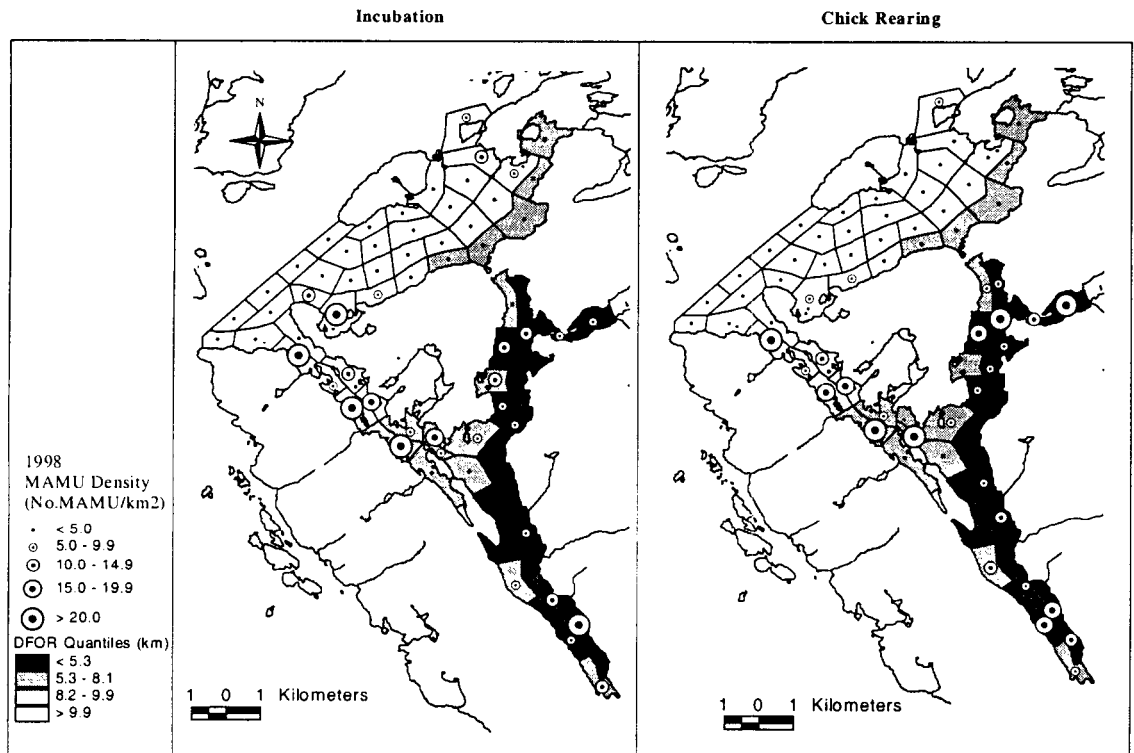


Figure 3.12. Diurnal and nocturnal proportion of inlet use. A lower proportion of birds were located in the inlets at night, indicating a general daily movement in and out of the inlets.

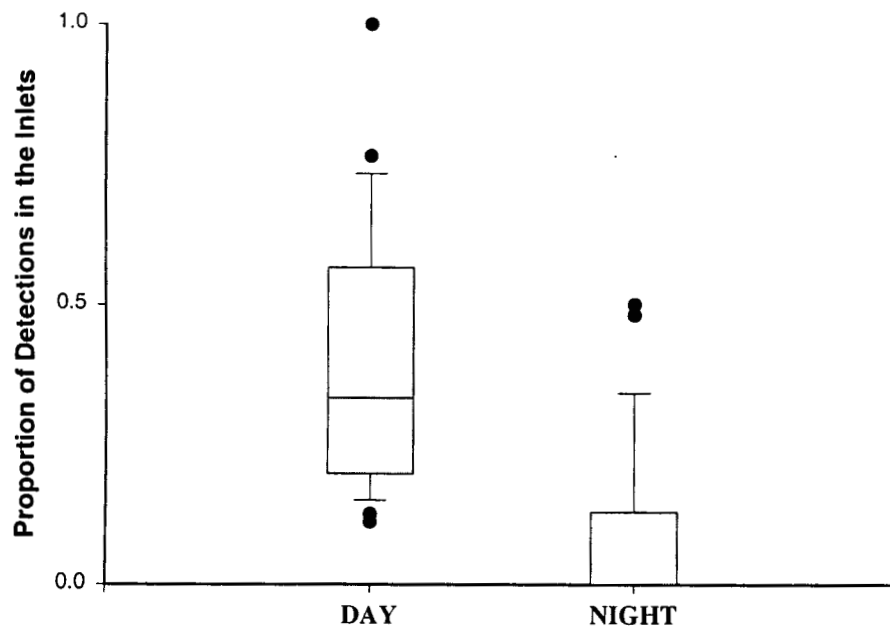


Figure 3.13. Diurnal activity centres for breeding Marbled Murrelets during pre-breeding and incubation, 1998.

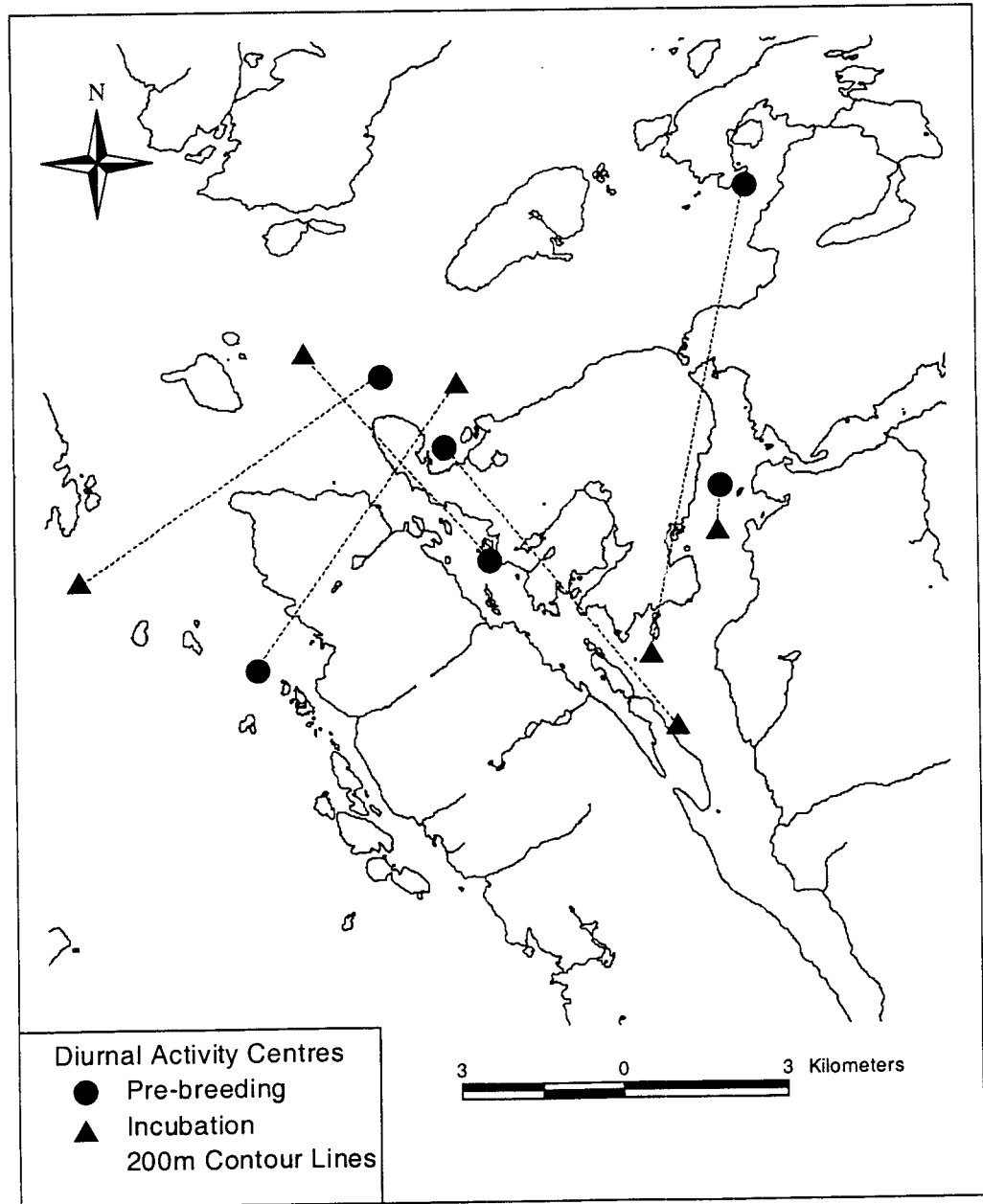


Figure 3.14. Diurnal activity centres for breeding Marbled Murrelets during incubation and chick rearing, 1998.

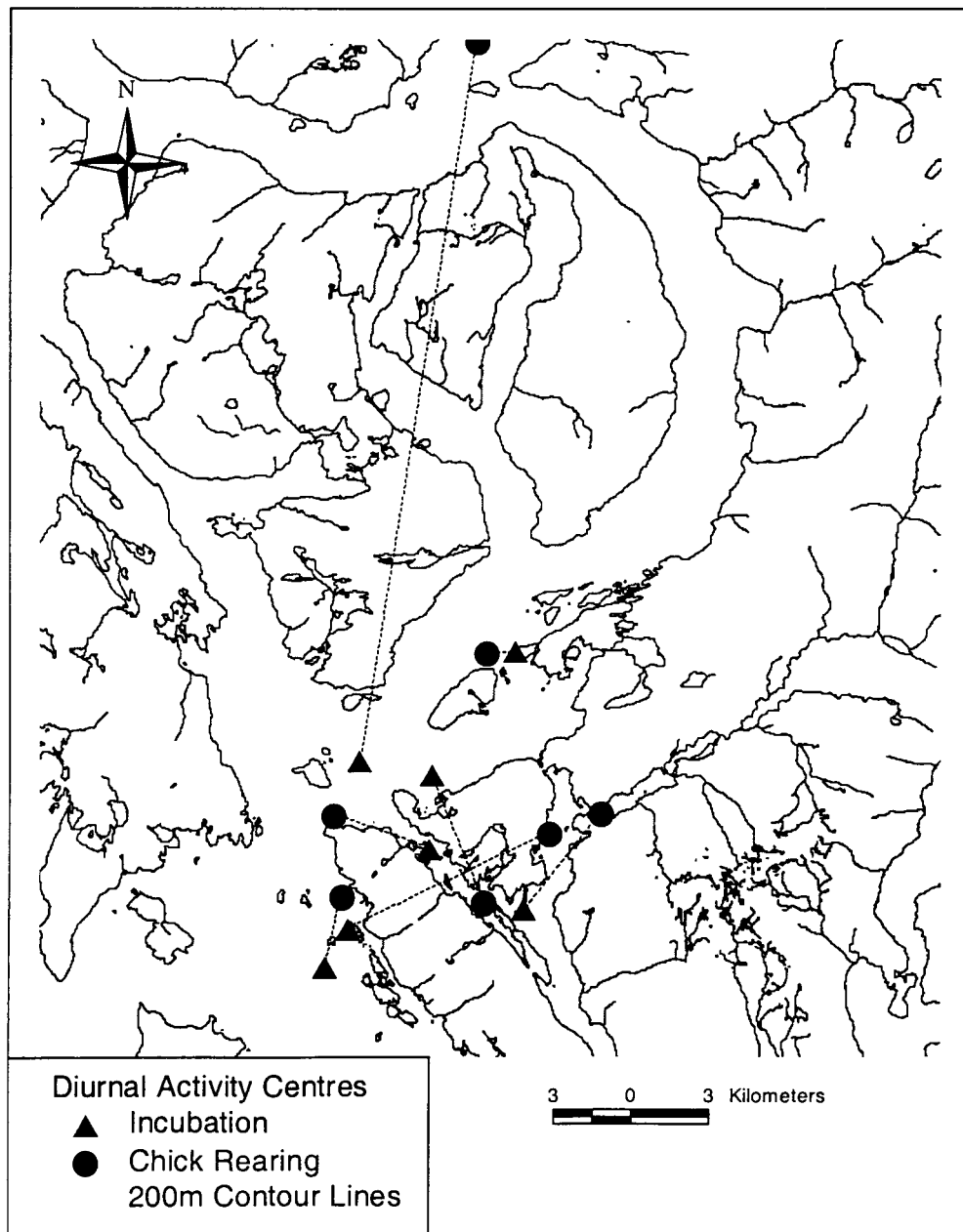
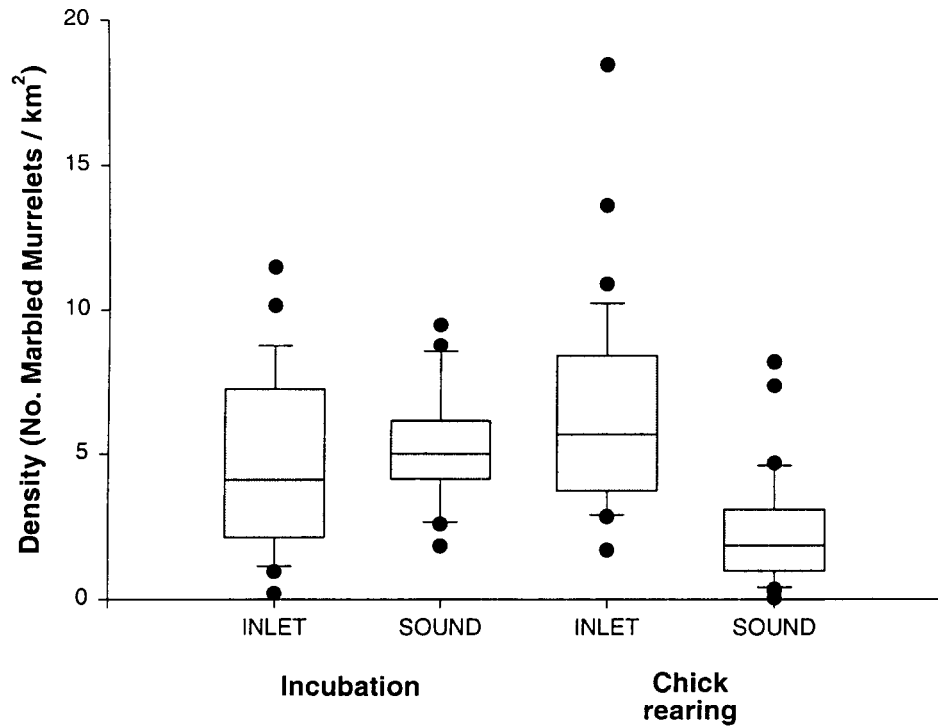


Figure 3.15. Density of Marbled Murrelets at two breeding stages (incubation and chick rearing) in the inlets and Desolation Sound. The patterns of use of the inlets and the Sound changed with breeding chronology. There were significant interactions between location (inlets and Sound) and breeding chronology ($F_{1, 105} = 25.98, P < 0.001$); which reflects birds moving into the inlets during chick rearing.



Discussion

The Marbled Murrelets are not randomly distributed throughout the marine areas of Desolation Sound; they move between habitats daily and seasonally. At the population level, distribution and habitat preference were dependent on breeding chronology period (incubation or chick rearing). At the individual level, I discovered that Marbled Murrelets undertake diel and seasonal movements. Neither diel, nor seasonal shifts in distribution were related to sex, however, seasonal movements among breeders were related to breeding chronology period.

Sea-surface temperature and distance to the old-growth forest were identified as significant explanatory variables of murrelet density. In general, the coldest waters available were preferred, and the warmest waters available were avoided, except during incubation in 1996 when the reverse was true. Cold water is associated with ocean productivity (and thus prey density) because of the vertical mixing of cold, nutrient rich bottom water (Hunt and Schneider 1987). Warm, stratified water is much less productive (Hunt 1997). Seabird food fish often prey on plankton (such as Pacific sand lance) and are usually more abundant in productive waters (reviewed in Baird 1990). Pacific sand lance, which are the primary prey of Marbled Murrelets during the breeding season (Carter and Sealy 1990; Burkett 1995; Nelson 1997), are known to be sensitive to changes in water temperature, and are most active between 10 and 15 °C (Winslade 1974; Field 1988). Therefore, the association of murrelet distribution with cooler sea-surface temperature waters is most likely due to prey availability. Murrelet distribution was also dependent on distance to the forest. There was a shift in preference between incubation and chick rearing. Water areas located further from the forest were selected during incubation, and water areas located closer to the forest were selected during chick rearing on all occasions except during chick rearing in 1996 and incubation in 1998. In both instances, there was no significant preference for or avoidance of any particular distance to old-growth forest category (see Table 3.3). These changes in the relationship between density of Marbled Murrelets and either sea-surface temperature or distance to the old-growth forest were clearly demonstrated by studying the changes in the slope of the regression (β) of habitat variable vs. murrelet density for each individual survey throughout the breeding season. A polynomial equation fit the change in estimates of β , that is, β gradually changed from positive early in the season, to negative, and then started to switch back to positive towards the end of the breeding season (Fig. 3.5, except 1996, Fig. 3.5b). The negative correlation became stronger during chick rearing. Finally, murrelet density was higher in Desolation Sound during incubation, but higher in the inlets during chick rearing, indicating a shift in location between the two breeding periods. Other variables than could explain the distribution of seabirds include, tidal condition, water depth and bottom profile (Hunt 1997).

In 1996, the average sea-surface temperature was the lowest of the three years of the study, and it was in this year that murrelet habitat selection was most uncertain. Although there was a negative correlation between season average SST and murrelet density, the decrease in $\beta_{\text{(SST vs. density)}}$ was weakest in 1996, and, unlike other years, neither SST nor DFOR explained significant variation in murrelet numbers during either of the crucial breeding stages (incubation and chick rearing). It was also during 1996 that murrelets had the best breeding success (see Chapter 2). It may be that because of the larger areas of cooler water, schools of prey were more spread out and murrelets did not have to concentrate in specific areas in order to find suitable prey. Thus, higher energetic costs of commuting to the nests may have been compensated for with increased availability of prey.

The study of individually marked birds provided further evidence that Marbled Murrelets moved to waters closer to the nest in response to the energetic demands of chick rearing. Seasonal movements were related to breeding status and breeding chronology. When they made the transition from incubation to chick rearing, breeding murrelets tended to shift their water locations to areas about 8.5 km closer to their nests. To avoid the potential biases due to the limited range of boat based telemetry, I used both boat and aerial telemetry to better assess the location of foraging areas. Changes in foraging areas could be related to prey availability or it could be a strategy to reduce energy expenditure related to the cost of commuting to the nest during chick rearing, which is the most energetically demanding period. Hull *et al.* (submitted) estimated that for murrelets the energetic cost of commuting increased during the breeding season, which was a result of an increase in the frequency of adult visits to the nests. There were also differences in location at sea related to breeding status. Breeders used the inlets to a greater degree than non-breeders; non-breeders were less likely to be found in the inlets than breeding birds.

I also document, for the first time, diel shifts in at-sea distribution of Marbled Murrelets, with birds moving away from the shoreline and out of the narrow inlets during the night. It is possible that the small diel adjustments in location are related to predation risk or that murrelets are moving away from shore to avoid being washed to the rocks while loafing at night. Birds may move away from shore and out of the inlets at night to reduce exposure to nocturnal predators that do not venture far from shore, such as owls or mink. Although there is no evidence that they prey upon murrelets, owls have been observed flying over the water nearshore at night in the study area (G. Keddie, pers. comm.). An alternative explanation is that birds were shifting locations between day and night to follow prey. Although in Desolation Sound there is no evidence that radio-tagged birds were diving at night (C. Lougheed pers. obs), it has been suggested that Marbled Murrelets feed at night (reviewed in Nelson 1997). Sandlance have traditionally been thought to be inactive at night (Field 1988) but others have noted night time sand lance activity (Carter and Sealy 1990). The movement away from

shore was significant for both breeders and non-breeders, however, breeders were located significantly further from shore than non-breeders.

Murrelets of both sexes had similar distributions during incubation and chick rearing, and both sexes used inlets during the day and vacated the inlets at night. This lack of difference between sexes is not surprising, because Marbled Murrelets are sexually monomorphic and seemingly share equally in both incubation and chick rearing (Nelson 1997).

By adjusting their local distribution at sea towards areas closer to their nesting grounds, Marbled Murrelets may be attempting to reduce energetic costs (of commuting and provisioning) during periods of high energy demand throughout the breeding season. This hypothesis is supported by the negative correlation between DFOR and murrelet density during chick rearing and by the movement of breeding birds to water areas closer to the nest during chick rearing. The negative relationships between SST and density (see above) during the breeding season also suggest that murrelets might be moving to take advantage of prey concentrations. If the birds that moved with the onset of chick rearing were only tracking a moving resource, then one would expect that non-breeding murrelets would use the inlets in similar proportions to breeders, but this was not the case. One would also expect murrelet density to be highest in areas with the lowest SST. The inlets were cooler than the Sound throughout the breeding season, however, murrelet density shifted between inlets and Sound (from at-sea surveys) with breeding chronology periods. Murrelet densities were lower in the inlets during incubation, but were higher during chick rearing. There might be a risk of predation associated with using the inlets. Marbled Murrelets may need to use the inlets to either reduce the cost of energy spent commuting to and from the nest or to meet energy demands of self-provisioning and chick-provisioning. Bald Eagles and seals are diurnal predators of Marbled Murrelets at sea (Nelson 1997), and both are abundant in the inlets of the study area (C. Lougheed pers. obs.). My data are consistent with the hypothesis that there is a trade-off between the use of risky, more productive waters located close to the nest and safer, more distant (and potentially less productive) waters. This implies that water areas close to old-growth suitable for nesting (i.e., the inlets of the Desolation Sound region) provide important habitat for foraging, especially during chick rearing. If the birds are stressed by breeding, these important marine areas should be protected from human disturbances such as recreational boating, shoreline development or mariculture.

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Appendix 3.1. Differential use of marine habitat between incubation (INC) and chick rearing (CR) by Marbled Murrelets, based on sea-surface temperature (SST). Temperature was divided in 4 categories, 1=cold, 4=warm.

Year	Chronologic al Stage	SST Category	Polygon Area in Category	Number of MAMU	Expected Proportion	Observed Proportion	Lower 95 CI	Upper 95 CI	Conclusion	Significant (*)
1996	INC	1	25.775	97.577	0.514	0.369	0.311	0.428	Under	*
1996	INC	2	14.003	74.513	0.279	0.282	0.228	0.336	Expected	
1996	INC	3	9.329	87.397	0.186	0.331	0.274	0.388	Over	*
1996	INC	4	1.067	4.654	0.021	0.018	0.002	0.033	Expected	
1997	INC	1	6.049	51.909	0.121	0.215	0.163	0.267	Over	*
1997	INC	2	10.563	44.727	0.211	0.186	0.137	0.235	Expected	
1997	INC	3	21.290	88.091	0.424	0.366	0.305	0.426	Expected	
1997	INC	4	12.273	56.273	0.245	0.233	0.180	0.287	Expected	
1998	INC	1	21.230	166.667	0.423	0.598	0.540	0.655	Over	*
1998	INC	2	15.559	74.333	0.310	0.267	0.215	0.318	Expected	
1998	INC	3	8.619	27.333	0.172	0.098	0.063	0.133	Under	*
1998	INC	4	4.766	10.500	0.095	0.038	0.015	0.060	Under	*
1996	CR	1	5.940	59.000	0.118	0.245	0.191	0.299	Over	*
1996	CR	2	5.313	24.143	0.106	0.100	0.062	0.138	Expected	
1996	CR	3	5.175	13.571	0.103	0.056	0.027	0.085	Under	*
1996	CR	4	33.747	144.071	0.673	0.598	0.536	0.660	Under	*
1997	CR	1	0.961	9.857	0.019	0.058	0.023	0.094	Over	*
1997	CR	2	5.128	20.357	0.102	0.121	0.072	0.170	Expected	
1997	CR	3	5.951	30.500	0.119	0.181	0.123	0.239	Over	*
1997	CR	4	38.134	107.857	0.760	0.640	0.567	0.712	Under	*
1998	CR	1	0.648	14.000	0.013	0.048	0.023	0.072	Over	*
1998	CR	2	2.978	59.889	0.059	0.204	0.158	0.250	Over	*
1998	CR	3	46.549	220.286	0.928	0.749	0.699	0.798	Under	*

Appendix 3.2. Differential use of marine habitat between incubation (INC) and chick rearing (CR) by Marbled Murrelets, based on distance to old-growth forest (DFOR). DFOR was divided in 4 categories: 1=close, 4=far.

Year	Chronological Stage	DFOR Category	Polygon Area in Category	Number of MAMU	Expected Proportion	Observed Proportion	Lower 95 CI	Upper 95 CI	Conclusion	Significant (*)
1996	INC	1	12.203	25.897	0.243	0.098	0.062	0.134	Under	*
1996	INC	2	11.825	66.372	0.236	0.251	0.199	0.304	Expected	
1996	INC	3	14.229	87.949	0.284	0.333	0.276	0.390	Expected	
1996	INC	4	11.918	83.923	0.238	0.318	0.262	0.374	Over	*
1997	INC	1	12.203	43.182	0.243	0.179	0.131	0.228	Under	*
1997	INC	2	11.825	45.455	0.236	0.189	0.139	0.238	Expected	
1997	INC	3	14.229	67.636	0.284	0.281	0.224	0.337	Expected	
1997	INC	4	11.918	84.727	0.238	0.352	0.291	0.412	Over	*
1998	INC	1	12.203	76.167	0.243	0.273	0.221	0.325	Expected	
1998	INC	2	11.825	68.667	0.236	0.246	0.196	0.297	Expected	
1998	INC	3	14.229	73.333	0.284	0.263	0.211	0.315	Expected	
1998	INC	4	11.918	60.667	0.238	0.218	0.169	0.266	Expected	
1996	CR	1	12.203	46.929	0.243	0.195	0.145	0.245	Expected	
1996	CR	2	11.825	62.929	0.236	0.261	0.206	0.317	Expected	
1996	CR	3	14.229	67.571	0.284	0.281	0.224	0.337	Expected	
1996	CR	4	11.918	63.357	0.238	0.263	0.208	0.319	Expected	
1997	CR	1	12.203	62.786	0.243	0.372	0.299	0.445	Over	*
1997	CR	2	11.825	37.214	0.236	0.221	0.158	0.283	Expected	
1997	CR	3	14.229	34.643	0.284	0.206	0.145	0.267	Under	*
1997	CR	4	11.918	33.929	0.238	0.201	0.141	0.262	Expected	
1998	CR	1	12.203	114.111	0.243	0.388	0.332	0.444	Over	*
1998	CR	2	11.825	85.127	0.236	0.289	0.238	0.341	Over	*
1998	CR	3	14.229	59.619	0.284	0.203	0.157	0.249	Under	*
1998	CR	4	11.918	35.317	0.238	0.120	0.083	0.157	Under	*

Appendix 3.3. Average distances to the nearest shore for 255 day - night (DY-NT) water locations pairs from 36 Marbled Murrelets marked with radio transmitters. I defined a DY-NT pair as two consecutive observations at each time period (DY and NT), that is, a NT detection paired with a detection from either the previous DY or the following DY period. Because aerial telemetry took place only during day hours, only boat detections were included.

Bird id.	Sex	Distance to Shore (km)			Number of DY-NT Pairs
		Breeder (Yes/No)	Day	Night	
131	Female	No	0.542	0.313	6
151	Female	Yes	0.415	0.410	2
162	Female	No	0.585	0.910	2
171	Male	No	0.236	1.000	3
192	Male	Yes	0.658	0.926	5
213	Female	Yes	0.471	0.623	13
231	Male	Yes	0.280	0.697	3
251	Male	Yes	0.420	1.280	2
273	Female	Yes	0.692	0.626	5
312	Male	No	0.178	0.693	6
322	Female	No	0.245	0.355	2
332	Male	No	0.312	0.909	17
365	Female	Yes	0.572	0.503	8
373	Female	No	0.317	0.423	4
383	Female	Yes	0.263	0.767	6
394	Female	Yes	0.189	0.712	9
412	Male	No	0.295	0.382	26
422	Female	No	0.726	0.743	3
432	Female	Yes	0.720	0.560	3
443	Male	Yes	0.443	0.688	9
472	Female	Yes	0.293	0.655	8
503	Male	No	0.226	0.703	7
533	Female	Yes	0.474	0.679	12
545	Male	Yes	0.208	0.695	13
554	Female	Yes	0.325	0.465	4
562	Female	No	0.463	0.580	3
592	Male	Yes	0.242	0.878	14
612	Female	No	0.243	0.590	8
633	Male	No	0.423	0.416	3
680	Male	Yes	0.610	0.544	8
695	Female	Yes	0.535	0.617	10
703	Female	Yes	0.550	0.673	6
753	Male	Yes	0.473	0.721	11
772	Male	Yes	0.245	0.612	9
783	Unknown	No	0.256	0.523	3
792	Female	No	0.315	0.420	2

General Discussion

This thesis contains unique information about Marbled Murrelet breeding chronology, local movements, and determinants of their at-sea distribution. I studied the murrelet population at Desolation Sound, British Columbia from 1996 to 1998. In general, I found that movements and distribution of Marbled Murrelets in Desolation Sound change in relation to breeding chronology. The use of individually marked birds and the estimates of the breeding chronology allowed me to examine the movement data in much finer detail, and revealed interesting seasonal patterns.

My results showed that the Marbled Murrelets in Desolation Sound bred from April 21 to September 5 on average (Chapter 1). Core incubation was mostly in June, and core chick rearing was mostly in July. I found that methods that allow analysis of the frequency distribution of the breeding events (such as physiological analysis, telemetry monitoring of breeding activities, and HY counts at sea) conducted throughout the breeding season, are better for assessing breeding chronology than single events (such the first observation of fish-holding behaviour, or first observation of a juvenile at sea). I also found that the breeding seasons were progressively earlier from 1996 to 1998, and that there was a parallel trend towards warmer average sea surface temperatures. This was the first evidence of interannual variation in timing of breeding for a Marbled Murrelet population.

The Marbled Murrelet breeding season in Desolation Sound was more asynchronous than predicted (based on measurements of other alcids) at this latitude. Alcids tend to breed more synchronously at higher latitudes (Gaston and Jones 1998). The same pattern of shorter breeding seasons with increasing latitude has been observed for Marbled Murrelets, with longest and earliest breeding seasons in California, and shortest and latest in Alaska (Nelson and Hamer 1995). Marbled Murrelet breeding asynchrony might be a response to both its solitary nesting habits and the seasonal (temporal) availability of prey (Kaiser 1994). If this is the case, prey is likely available for a longer period for murrelets than that of other alcids.

Early in this study, I designed an at-sea survey that covered most of the Desolation Sound area. In 1998, adult emigration (measured with radio-tagged individuals) out of the survey area was low during incubation and early chick rearing, confirming that birds using that area are residents, rather than transients (Chapter 2). In contrast, juvenile emigration was higher than that of AHY birds, with very few individuals remaining in the area over a week. I used this information to calculate juvenile ratios, which are assumed to be good estimates of fecundity (Beissinger 1995; Kuletz and Kendall 1998). Despite my corrections, juvenile ratios were lower than independent estimates of fecundity based on nest site monitoring. This could be explained by either an unexpectedly high proportion of non-breeding age AHY birds (subadults) in the surveys

counts, or differential use of habitat by adults and juveniles. I believe that counts from at-sea surveys include breeding adults that nest over a wide area, but will only include juveniles from nest sites in the local hills and drainages. I found that the timing of the peak number of AHY birds fluctuated across years, which might result in an uncorrectable bias in the counts. An accurate estimate of the number of AHY birds is essential for the calculation of representative juvenile ratios. The results of this study suggest that caution must be used when interpreting juvenile ratios from at-sea surveys.

My results demonstrate that there were distinct trends in population movements throughout the breeding season (Chapter 3). There was a general shift in habitat use between incubation and chick rearing. Changes in densities of Marbled Murrelets were generally related to sea-surface temperature and distance to the nearest patch of old-growth forest. The analyses of the slope of regressions of murrelet density and habitat variables (β) during the breeding season, demonstrates the changing relationships among murrelet density and habitat variables. The relationships gradually changed from positive to negative (preference for cooler waters, closer to the forest) but then the trend reversed and β become increasingly positive as the end of the breeding season approached. This means, because the population is largely resident, that the birds moved closer to the forest, especially during chick rearing. The only year that did not follow this pattern was 1996, and was characterized by the coldest water and the best breeding success (see Chapter 2). It seems logical that if sandlance are occupying cold waters (Winsdale 1974; Field 1988; Quinn and Schneider 1991), murrelets would concentrate there in years in which that type of water was scarce.

I was able to confirm these general patterns of movements using individually radio-tagged birds. As expected, the breeding individuals tended to alter their centres of activity toward nesting areas during chick rearing. In addition, I determined that the murrelets that use the inlets during the day move out of the inlets at night, and that overall more breeding birds use the inlets than non-breeding birds. Generally, birds moved away from the shore during the night. Taken together, this body of evidence of the seasonal movements of Marbled Murrelets conform to the hypothesis that these patterns of movement and distribution reflect a trade-off between the use of productive but risky waters close to the shore or the nest and safer, more distant waters.

Conservation Implications

Understanding the ecology of Marbled Murrelets is complex, as for many threatened species, because of difficulties in data collection. Studying Marbled Murrelets at the nest site with methods traditionally used for colonial seabirds is not feasible because of the inaccessibility of nest sites, their cryptic nature, concerns about disturbance to nesting adults, and the attraction of

predators. These make alternate methods of studying characteristics of the murrelet population extremely valuable. In an attempt to understand murrelet biology in the face of sparse data, researchers have been obliged to pool data across years and populations. This is troublesome for two reasons: (1) trends are masked and (2) different populations may have different characteristics. My investigations are unique in that they were conducted on a single population in a way that allowed me to interpret seasonal and annual trends of important characteristics. Monitoring populations at sea to determine productivity has been highlighted as one of the priorities for the determination of murrelet demography (Nelson 1997). I demonstrate how local movements of hatch year and after-hatch year birds could influence the estimates of juvenile ratios from at-sea counts. Juvenile ratios are commonly used as estimates of fecundity (Kuletz and Kendall 1998) and are used in recovery plans (U.S. Fish and Wildlife Service 1997). I point out that at-sea estimates of productivity (juvenile ratios) must be used with caution because there are unknown biases inherent in the process that may mask the true variation needed to assess long term population trends.

My investigations have contributed valuable information regarding Marbled Murrelet breeding biology and marine habitat selectivity. The information about the relationships among local movements, marine habitat selectivity, breeding chronology, and breeding status provided by this study highlights the importance of high productivity marine areas located close to the nesting grounds. The marine habitat, therefore, must be considered by managers when deciding on conservation strategies, such as land use planning for Marbled Murrelet nesting habitat. If the marine environment used by Marbled Murrelets is not protected at the same time as forest patches for nesting are set aside, the murrelet population could suffer reduction in food availability or high human disturbance during crucial stages of the breeding cycle. Activities that contribute to marine habitat degradation (pollution, and bioaccumulation of toxins) such as shoreline development, oil transport, or pulp mills could affect the availability of food resources (Carter and Kuletz 1995; Speckman 1996). For example, DDE pollution in the southern California Bight was responsible for poor reproductive success and population declines in Brown Pelicans and Double-crested Cormorants (Gress *et al.* 1973; Anderson *et al.* 1975). Not protecting the marine habitat of the Marbled Murrelet would cause low reproductive success and eventually will result in population declines, wasting the efforts of land use planners.

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