



Estimating 30-year change in coastal old-growth habitat for a forest-nesting seabird in British Columbia, Canada

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ABSTRACT: The marbled murrelet *Brachyramphus marmoratus* is an old-growth dependent species that nests in North American coastal forests. Canadian populations and occurrence data are limited; however concern over loss of nesting habitat in coastal British Columbia led to an assessment of 'threatened' by the Committee on the Status of Endangered Wildlife in Canada, and subsequent listing under the Canadian Species at Risk Act. Information on the availability and patterns of change in nesting habitat is essential for making land-use decisions and for monitoring the conservation status of this wide-ranging seabird. We estimated potential marbled murrelet nesting habitat for the coast of British Columbia at 2 points in time, 1978 and 2008, and quantified habitat loss and modelled habitat recruitment over this 30 yr time period, a key time frame for the assessment of the conservation status of this high-profile species. We implemented 3 predictive habitat suitability models for the province of British Columbia, ranging from exclusive to more inclusive models. Based on the various habitat model scenarios, including corrections using aspatial harvest records, we estimated that 20 to 24 % of potential marbled murrelet nesting habitat was lost to forest harvest and fire from 1978 to 2008. If modelled habitat recruitment is considered, then net change in potential nesting habitat is 20 to 22 % loss. Our estimates of potential murrelet habitat and subsequent habitat loss and change are influenced by numerous sources of uncertainty, such as actual suitability of forest stands for breeding murrelets and known deficiencies in the forest harvest spatial datasets. However, the results presented here provide the first range of province-wide habitat change possibilities and are consistent with previous regional analyses of potential marbled murrelet habitat loss in British Columbia.

KEY WORDS: Marbled murrelet · *Brachyramphus marmoratus* · Nesting habitat · Spatial modelling · Habitat loss · British Columbia · Geographic information systems · GIS

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INTRODUCTION

Marbled murrelets *Brachyramphus marmoratus* are small seabirds that live along the northern Pacific coast of North America. Unlike typical members of the Alcidae family, marbled murrelets nest primarily in the trees of coastal old-growth forests (Burger 2002, Piatt et al. 2007). The distribution of marbled murrelets ranges from northern California to Alaska, with larger

murrelet populations found at higher latitudes and the majority of the global population found in Alaska (Piatt et al. 2007). It is estimated that British Columbia, the sole range of breeding marbled murrelets in Canada, is home to approximately 99 600 marbled murrelets (72 600–125 600, Bertram et al. 2007). Details of the spatial distribution of the murrelet population within British Columbia are limited; marine environments have not been systematically surveyed across the

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province (but see Yen et al. 2004), and their cryptic nesting behaviour makes them difficult to study, especially in remote terrestrial locations (Canadian Marbled Murrelet Recovery Team, CMMRT 2003). While marine surveys, along with historical anecdotes of abundance, have suggested a sharp decline in marbled murrelet populations in some areas, other data suggest some stable populations in British Columbia (e.g. Kelson et al. 1995, Burger 2002, Lank et al. 2003, Piatt et al. 2007). However, historical information on the number of marbled murrelets in British Columbia and population or demographic data are limited for this elusive species (CMMRT 2003).

The Canadian population of marbled murrelets was assessed as 'threatened' by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2000), resulting in the legal listing of the marbled murrelet under the Canadian Species at Risk Act. With limited information on population status (e.g. decline of mature individuals), the Canadian marbled murrelet conservation assessment was based on an estimated reduction in the extent of old-growth forest nesting habitat in coastal British Columbia over approximately 30 yr, or 3 generations, a standardised time window for species conservation assessments (COSEWIC 2000, IUCN Standards and Petitions Subcommittee 2010). Loss of terrestrial nesting habitat is considered the primary threat to marbled murrelet populations range-wide (CMMRT 2003, Piatt et al. 2007) and is well supported by the literature (e.g. Burger 2001, 2002, Raphael et al. 2002, Piatt et al. 2007, Burger & Waterhouse 2009). Other threats to population persistence occur in the marine environment, including fisheries by-catch and oil spills (CMMRT 2003). In addition, recent research has highlighted the potential role of historical depletion of food supply (i.e. fisheries) in marbled murrelet declines and/or the potential for population recovery (e.g. Becker & Beissinger 2006, Becker et al. 2007, Beissinger & Peery 2007, Norris et al. 2007, Gutowsky et al. 2009).

Marbled murrelet nesting habitat has been well characterised at landscape, stand, tree and platform levels (e.g. Burger 2002, Piatt et al. 2007, Burger et al. 2010). Marbled murrelet nests are typically found in trees with large branches and sufficient epiphytic growth (e.g. Burger et al. 2010), characteristics that are usually found in relatively older and taller trees (e.g. >250 yr, >28.5 m high, Burger 2002). Associations of nest sites with other macro-habitat features, such as elevation and distance to sea, have also been investigated in order to characterise suitable habitat over increasing scales (Burger 2002). Nest trees are generally found up to 50 km inland, but mostly within 30 km from the shoreline (Burger 2002), as these seabirds are limited by the commuting distance from foraging areas (Hull et al. 2001).

Quantifying the degree of change in available marbled murrelet old-growth nesting habitat through time is necessary for characterising present, and predicting future abundance of marbled murrelets in British Columbia, assuming that terrestrial habitat is a key predictor of population abundance and an indicator of the likelihood of local population persistence (e.g. Burger 2001, Steventon et al. 2003, Burger & Waterhouse 2009). Recent research efforts have produced regional- and broad-scale estimates of potential murrelet nesting habitat for single time periods (e.g. Waterhouse et al. 2008, 2009, Mather et al. 2010), as well as a few regional-scale or shorter time-frame analyses estimating change in available murrelet habitat (e.g. Gowgaia Institute 2007, M. Tomlins & M. Gray unpubl.).

Here we used geographic information systems (GIS) and habitat suitability modelling techniques to implement a set of 3 spatially explicit, province-wide terrestrial marbled murrelet habitat models. We also estimated the amount of forest disturbance from forest harvest and fires, and resulting change in availability of predicted marbled murrelet nesting habitat over a 30 yr period for the entire coast of British Columbia. We mapped forest conditions in 2 time periods, 1978 and 2008; applied 3 predictive marbled murrelet nesting habitat suitability models to estimate the amount of nesting habitat available for the years 1978 and 2008, quantified the amount of loss from forest harvest and fire; and finally, calculated net change, assuming modelled recruitment of suitable nesting habitat between 1978 and 2008. The results presented here provide the first province-wide account of spatially explicit habitat change scenarios, and we discuss the benefits and limitations of a spatially explicit approach for deriving estimates of species habitat change over large areas.

MATERIALS AND METHODS

Study area. The study area includes the entire coast of British Columbia, the current range of the breeding population of marbled murrelets in Canada (CMMRT 2003). The study area is divided into 6 conservation regions of different sizes: West and North Vancouver Island (2.15 million ha); East Vancouver Island (1.15 million ha); Southern Mainland Coast (3.97 million ha); Central Mainland Coast (4.21 million ha); Northern Mainland Coast (5.61 million ha); and Haida Gwaii (1 million ha; Fig. 1). These regions were developed by the CMMRT and are based on forest districts, land and wildlife management regions, and ecosection boundaries (CMMRT 2003). Each conservation region differs in the current estimated abundance of marbled murrelets and in conservation priorities (CMMRT 2003).

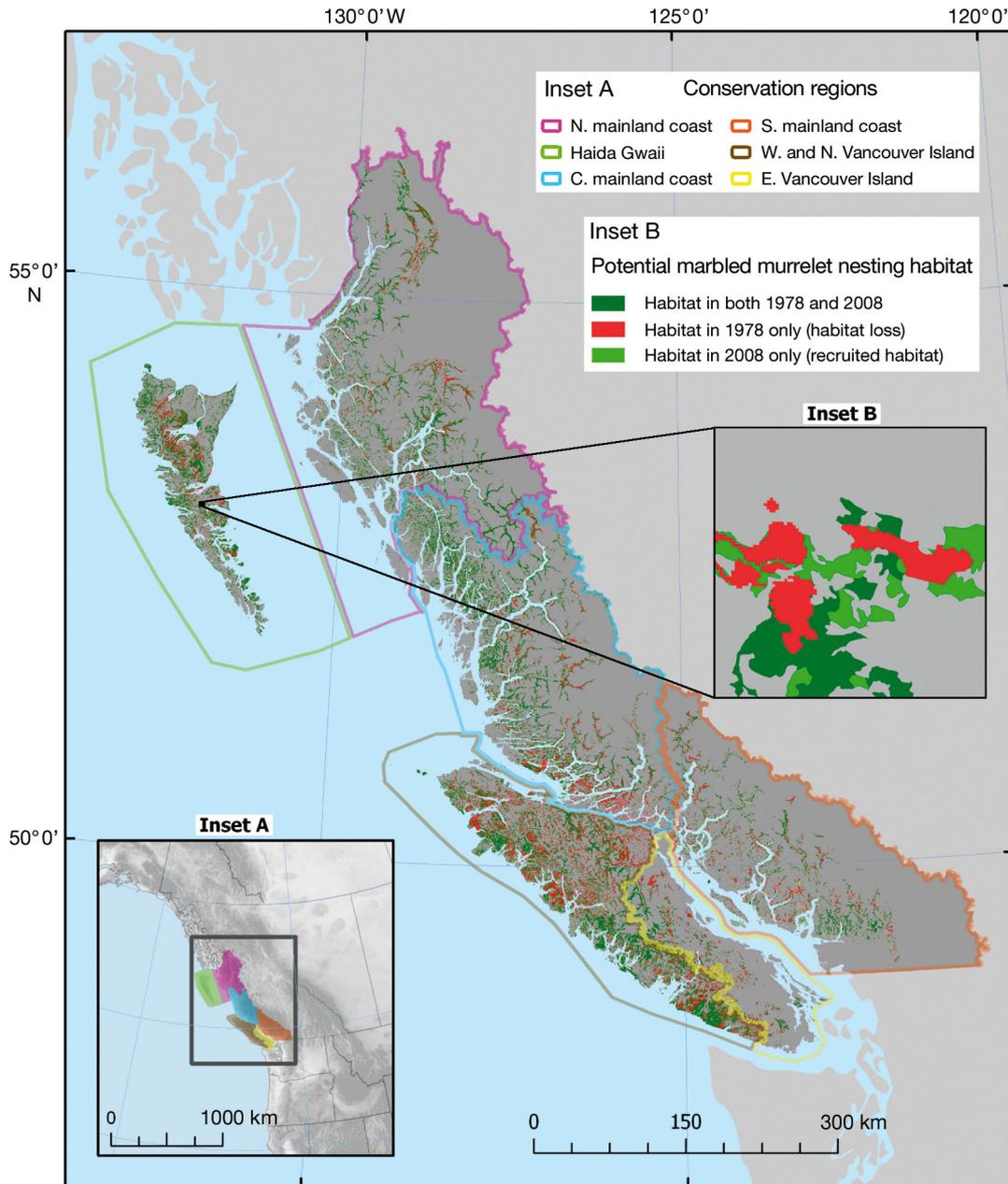


Fig. 1. Six conservation regions for management of old-growth marbled murrelet *Brachyramphus marmoratus* nesting habitat in British Columbia (Inset A), with results from analysis of changes in potential nesting habitat area (main map) using the intermediate (Model 2) definition of habitat. Example of detailed view of habitat results provided in Inset B

Marbled murrelet nesting habitat model selection.

Several predictive attributes and models of potentially suitable marbled murrelet nesting habitat have been developed for British Columbia (e.g. McLennan et al. 2000, Bahn & Newsom 2002, CMMRT 2003, Chatwin & Mather 2007, Mather et al. 2010). All predictive habitat models carry some degree of uncertainty, due, for example, to limited or poor quality input data (e.g. Waterhouse et al. 2010). In an attempt to account for the influence of model uncertainty, we implemented

3 predictive marbled murrelet habitat suitability models. The 3 models reflect a range of predictive scenarios of potential marbled murrelet nesting habitat from an exclusive model (Model 1; CMMRT 2003), an intermediate model (Model 2; Mather et al. 2010), to an inclusive model (Model 3; CMMRT 2003). All 3 models use 4 key environmental variables (forest height, forest age, elevation and distance from nearest ocean shoreline; Table 1), which are appropriate for large-area modelling of potential marbled murrelet nesting habitat.

Table 1. Marbled murrelet nesting habitat attributes for each of 3 habitat suitability models. Model 1 is the most exclusive, Model 2 is intermediate, and Model 3 is the most inclusive, in terms of definition of potential marbled murrelet nesting habitat

Attributes	Model 1	Model 2	Model 3
Forest stand age (yr)	≥250	≥140	≥140
Forest stand height (m)	≥28.5	≥28.5	≥19.5
Distance to ocean shoreline (km)	0.5–30	0–50	0–50
Elevation (m)			
Central & Northern Mainland Coast	≤600	≤600	≤900
Haida Gwaii	≤500	≤500	≤800
All other regions	≤900	≤900	≤1500

Model 1, based on guidelines developed by the CMMRT (2003), uses the most exclusive definition of potential marbled murrelet nesting habitat. Model 1 is equivalent to the CMMRT's estimate of 'most likely' habitat, where habitat is considered potential marbled murrelet nesting habitat if forest age is ≥250 yr, forest height is ≥28.5 m, and location is 500 m to 30 km from ocean shorelines. Elevation thresholds vary from ≤500 m to ≤900 m and depend on conservation region (Table 1). Model 1 indicates potential habitats considered most likely to provide suitable nesting habitat for marbled murrelets in British Columbia (CMMRT 2003).

Model 2 is the most common set of parameters used for estimating potential marbled murrelet nesting habitat in coastal British Columbia (Chatwin & Mather 2007, Mather et al. 2010, Waterhouse et al. 2010). Model 2 uses the attribute thresholds from Mather et al. (2010), which are based on a hybrid of the CMMRT's predicted 'most and moderately likely' guidelines for habitat attributes (CMMRT 2003). In this case, nesting habitat is modelled as locations with forests aged ≥140 yr, heights ≥28.5 m, and distance to ocean shoreline between 0 and 50 km (Table 1). Elevation classes associated with Model 2 are the same as with Model 1.

Model 3 employs the most inclusive definition of potential marbled murrelet nesting habitat, with a location considered potential marbled murrelet nesting habitat if it meets the requirements of the CMMRT's (2003) model for either 'most likely' or 'moderately likely' habitat. Forest age is ≥140 yr, forest height is ≥19.5 m, and location is 0 to 50 km from ocean shorelines. Elevation thresholds in Model 3 are higher than other models and range from ≤800 to ≤1500 m depending on conservation region (Table 1). Given the inclusivity of this parameter set, the recovery team recommended detailed ground-truthing of 'moderately

likely' habitats to ensure that these habitats contain the potential attributes required for nesting marbled murrelets (CMMRT 2003).

Data sources. The distance-to-ocean-shoreline variable was computed using British Columbia's baseline thematic mapping (BTM) data (British Columbia Ministry of Environment, Lands and Parks 1995). This dataset was derived using visual interpretation of Landsat satellite imagery from the early and mid-1990s and provides a coarse definition of British Columbia land cover and coastline. Included in this dataset is a saltwater map, from which distance-to-ocean-shoreline calculations were made. Using the BTM data, deep inlets, which occur regularly along the coast of British Columbia, are considered saltwater and were used in distance-to-ocean-shoreline calculations.

Elevation was determined using a digital elevation model (DEM), with a spatial resolution of 25 m. This DEM was created from 1:20 000 Terrain Research Information Management data (Province of British Columbia 1996) and is reported to be accurate within 10 m (British Columbia Ministry of Sustainable Resource Management 2002).

In British Columbia, the most complete dataset for mapping forest age and height variables is the forest inventory, which contains detailed age and height information on forest stands, is spatially continuous, and covers 90% of our study area. Regions excluded from the forest inventory data include privately owned timber land holdings, such as those along the southeast coast of Vancouver Island, as well as some park lands. Polygons, the spatial unit of the forest inventory, are used to represent forest stands (Leckie & Gillis 1995) and are commonly selected as the spatial unit for modelling marbled murrelet habitat over broad spatial scales (e.g. Chatwin & Mather 2007, Mather et al. 2010). In constructing the forest inventory, forest stand attributes were visually interpreted from aerial photographs. Stand age is the average age, in years, of the dominant and co-dominant trees in a forest stand and is typically estimated indirectly from aerial photographs. Stand ages are recorded as individual years, but also grouped into categories: 1–20, 21–40, 41–60, 61–80, 81–100, 101–120, 121–140, 141–250, and >250 yr. Interpretation of individual stand age becomes increasingly difficult as forests reach maturity; as such, category midpoints are often assigned as the forest age for the individual year attribute (Wong et al. 2003). We used individual stand age in our analysis. Stand height was interpreted directly from the aerial photograph and reported in metres.

For the remaining 10% of the study area, where forest inventory data are unavailable, BTM data (British Columbia Ministry of Environment, Lands and Parks 1995) were used. BTM data provide broad information

on stand age, reported as age categories: old forest (>140 yr), young forest (20–140 yr) and recently harvested (<20 yr). Height variables are unavailable with the BTM data, but it was assumed that old forest stands were also of suitable height for marbled murrelet nesting habitat.

Sources of change to potential marbled murrelet nesting habitat. Since our goal was to estimate change in potential marbled murrelet habitat between 1978 and 2008, we required data for each environmental variable at each time period. Distance to ocean shoreline and elevation do not change between time periods. As forest stands age, height growth slows, reaching a constant once mature (Ryan & Yoder 1997). Given the broad height classes used in marbled murrelet habitat modelling, height changes have little impact on model estimates and therefore were treated as static in the analysis. Forest stand ages were modelled dynamically, changing stand age appropriately from 1978 to 2008.

Forest disturbances, including those from both anthropogenic (e.g. harvest) and natural (e.g. fire) causes, represent the primary sources of loss to potential marbled murrelet nesting habitat (CMMRT 2003). The forest inventory and BTM datasets have not been judiciously updated and are missing many forest disturbances from 1978 to 2008. Thus, it was necessary to look to other data sources to obtain complete forest disturbance records. Spatially explicit forest disturbance data are available from a variety of data sources (Table 2). Due to known deficiencies (both spatial and

temporal), we complemented the available forest disturbance data with a Landsat-based change detection method using the enhanced wetness difference index (EWDI). The EWDI is based on the wetness component of the tasselled cap transformation and can be used to spatially identify large forest disturbances (Franklin et al. 2001, 2002). We restricted our analysis to those disturbances >1 ha to align with existing disturbance datasets (A. Morrison pers. comm.). All forest disturbance data (Table 2) were combined to create a single, spatially explicit forest disturbance dataset for 1978 to 2008.

Landsat imagery is unavailable prior to 1985 and thus our method using Landsat imagery to fill in gaps could not be used from 1978 to 1985. We therefore drew upon aspatial harvest records for 1978 to 1985 to improve our calculation of forest disturbance and subsequent estimates of potential marbled murrelet nesting habitat loss.

Estimating change in modelled nesting habitat. We combined the forest inventory data with forest disturbance data using appropriate GIS operations (Fig. 2) to derive forest attribute datasets for 1978 and 2008. Forest attribute data for 1978 and 2008 are combined with distance-to-ocean-shoreline and elevation data to implement the 3 marbled murrelet nesting habitat models (Fig. 2).

When forest age is included in a habitat model, there are 2 approaches to modelling habitat loss. Habitat loss can be modelled as the amount of habitat observed in the initial time period (1978) minus the amount of habi-

Table 2. Data sources used in derivation of 1978 and 2008 potential marbled murrelet nesting habitat. See Fig. 2 for a flow diagram demonstrating how all datasets are integrated into the analysis. BC: British Columbia, TFL: tree farm licence

Dataset	Notes	Source
Forest inventory	Primary source of forest attribute information	BC Ministry of Forests and Range, Forest Analysis and Inventory Branch, Victoria, BC
Baseline thematic mapping (BTM)	Used in distance to ocean shoreline calculation and to supplement forest inventory	BC Ministry of Environment, Lands and Parks, currently housed with GeoBC, Integrated Land Management Bureau, Victoria, BC
British Columbia digital elevation model (DEM)	Elevation data (25 m resolution)	BC Ministry of Sustainable Resource Management, Base Mapping and Geomatics Services Branch, Victoria, BC
Forest disturbance data		
Vegetation Resources Inventory (VRI)	Available for 1978–2008, primary harvest data	Sandvoss et al. (2005)
RESULTS database	Available for 1980–2008, harvest data for TFLs	BC Ministry of Forests and Range, Forest Analysis and Inventory Branch, Victoria, BC
Change detection layer (CDL)	Available for 2000–2008, harvest data for private lands (>1 ha)	BC Ministry of Forests and Range, Forest Analysis and Inventory Branch, Victoria, BC
National Fire Database (NFD)	Available for 1978–2005, source of forest fire disturbances	BC Forest Service, Protection Branch, Victoria, BC, but also see Parisien et al. (2006)
Landsat change	Available for 1985–2008, used to fill known spatial/temporal gaps in other data sources	Present study

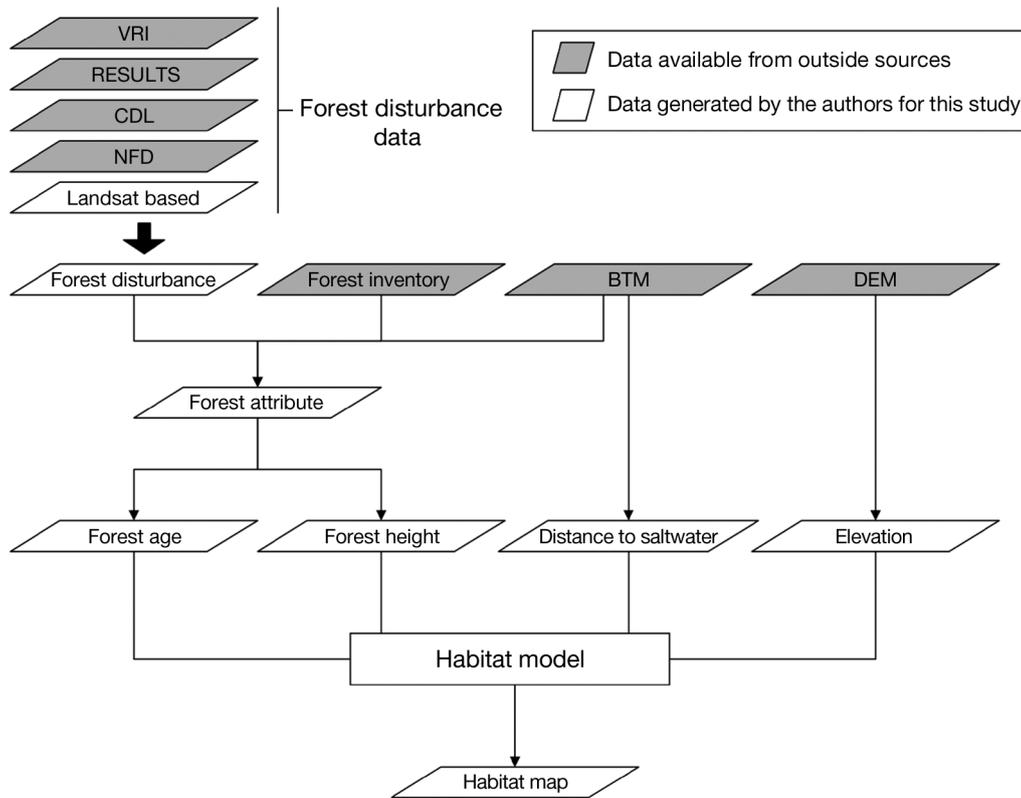


Fig. 2. Input data sources (see Table 2) are combined to generate datasets on environmental variables used in 3 marbled murrelet nesting habitat models. Abbreviations as in Table 2

tat lost between the first and second time periods (1978 and 2008). This approach does not consider increases to forest age and ignores the opportunity for new habitat to be recruited into potentially available classes over the study time period, in this case 30 yr. For instance, suitable habitat that was too young in 1978 crosses the model age threshold in 2008. In this example, recruitment of habitat is controversial as it represents the creation of new 'old-growth' forest. However, consideration of habitat recruitment is important as it preserves equivalent definitions of potential marbled murrelet habitat—from a data perspective—at both time points. We considered both types of analyses: habitat loss and net change in habitat, the latter including modelled habitat recruitment.

RESULTS

Marbled murrelet nesting habitat models

The predictive habitat models we implemented suggest that the spatial extent of potential marbled murrelet nesting habitat in 1978 covered 1.36 million to 4.70 million ha, depending on the model (Fig. 1, Table 3). The regional estimates of predicted marbled

murrelet nesting habitat varied by model, with either the West and North Vancouver Island region or Central Coast region containing the largest amount of predicted nesting habitat (Table 3). The spatial extent of predicted marbled murrelet nesting habitat in 2008 ranged from 1.29 million to 4.03 million ha, with the intermediate Model 2 predicting 2.1 million ha of available marbled murrelet nesting habitat in 2008 (Fig. 1, Table 3).

Marbled murrelet nesting habitat model loss

We spatially detected a total of 1.06 million ha of forest disturbance (from harvest and fire) within the study area from 1978 to 2008 (Fig. 1). Forest fires accounted for less than 5% of all disturbance area, occurring primarily at substantial distances from the ocean shoreline, making fire a relatively minor disturbance factor in this analysis. By area, 26% of all disturbances intersected Model 1 habitat in 1978, 50% intersected Model 2 habitat, and 73% intersected Model 3 habitat (Fig. 1, Table 3; 'Loss' column). Our estimates of marbled murrelet nesting habitat loss ranged from 16.3 to 20.6%, (Fig. 1, Table 3). Models 1 and 2 showed very similar percentages of overall habitat loss, 20.2 and

Table 3. Estimates of availability and changes to potential marbled murrelet nesting habitat in 1978 and 2008, using 3 habitat suitability models. Loss and recruitment represent negative and positive sources of change, respectively, to available habitat. Habitat loss is area of 1978 habitat that was lost by 2008 through forest disturbance. Habitat recruits from non-habitat in 1978 to Model 1 habitat in 2008 if, by aging for 30 yr, stand age crosses from <250 to ≥250 yr and satisfies the other requirements of the model. Habitat recruits from non-habitat in 1978 to Model 2 (or Model 3) habitat in 2008 if, by aging for 30 yr, stand age crosses from <140 to ≥140 yr and satisfies the other requirements of the model

Model Conservation region	Available habitat (ha)		Loss		Recruitment (ha)	Net change	
	1978	2008	ha	(%)		(ha)	(%)
Model 1							
West & North Vancouver Island	442613	384579	113316	(25.6)	55282	-58034	-13.1
East Vancouver Island	32145	27005	5416	(16.8)	276	-5140	-16.0
South Coast	139346	114329	38422	(27.6)	13405	-25017	-18.0
Central Coast	298887	330384	64212	(21.5)	95711	+31497	+10.5
North Coast	228680	243404	18512	(8.1)	33236	+14724	+6.4
Haida Gwaii	221183	188933	35407	(16.0)	3157	-32250	-14.6
Total	1362854	1288634	275287	(20.2)	201067	-74220	-5.4
Model 2							
West & North Vancouver Island	808345	591019	225685	(27.9)	8359	-217326	-26.9
East Vancouver Island	125054	91882	33918	(27.1)	746	-33172	-26.5
South Coast	240394	200990	62438	(26.0)	23034	-39404	-16.4
Central Coast	630197	526622	112365	(17.8)	8790	-103575	-16.4
North Coast	475090	431566	52858	(11.1)	9334	-43524	-9.2
Haida Gwaii	310635	267859	45095	(14.5)	2319	-42776	-13.8
Total	2589715	2109938	532359	(20.6)	52582	-479777	-18.5
Model 3							
West & North Vancouver Island	1139886	846355	304271	(26.7)	10740	-293531	-25.8
East Vancouver Island	198840	151043	48657	(24.5)	860	-47797	-24.0
South Coast	566278	502973	98485	(17.4)	35180	-63305	-11.2
Central Coast	1253628	1105271	164345	(13.1)	15988	-148357	-11.8
North Coast	1033029	968185	85998	(8.3)	21154	-64844	-6.3
Haida Gwaii	512357	452934	66763	(13.0)	7340	-59423	-11.6
Total	4704018	4026761	7568519	(16.3)	91262	-677257	-14.4

20.6%, respectively. Regionally, percent habitat loss using each of the 3 models was also similar, except for East Vancouver Island (16.8 to 27.1%) and the South Coast (17.4 to 27.6%; Table 3). Generally, estimated habitat loss was highest in the West and North Vancouver Island conservation regions, regardless of the model (25.6 to 27.9%). Predicted amounts of habitat loss were also high in the South Coast (17.4 to 27.6%) and East Vancouver Island conservation regions (16.8 to 27.1%), depending on the habitat model (Table 3).

Marbled murrelet nesting habitat model recruitment

Modelled habitat recruitment, based on forest aging over 30 yr, had a varied impact on model outputs (Fig. 1, Table 3; 'Recruitment' column). Models 2 and 3, both with thresholds for potentially suitable nesting habitat using ≥140 yr forest age, had relatively similar estimates of modelled habitat recruitment, with ~2% of the 2008 predicted available habitat resulting from modelled recruitment (52 582 and 91 262 ha, respectively; Table 3). Model 1, which was the most exclusive

estimate of potential habitat with a forest age threshold for nesting habitat of ≥250 yr, had the most recruitment with ~15% of the 2008 potential habitat resulting from recruitment (201 067 ha; Table 3). Regionally, Model 2 and Model 3 had different overall amounts of recruitment, but similar general patterns. For example, the highest (South Coast) and lowest (East Vancouver Island) amount of modelled habitat recruitment were the same for both models (Table 3).

Marbled murrelet nesting habitat model change

Throughout British Columbia, the percentage change in potential marbled murrelet nesting habitat, considering both habitat loss from harvest and fire and modelled habitat recruitment, varied from -5.4 to -18.5% depending on the model (Table 3; 'Net change' column). Model 1, which had the most recruitment, showed the smallest amount of change (-5.4%); Model 2 showed the most change (-18.5%); Model 3 showed moderate change at -14.4% (Table 3). Again, regional trends associated with change were variable

across models. According to Model 1, the South Coast has had the greatest net loss in potential marbled murrelet nesting habitat (–18.0%). For Models 2 and 3, net loss was greatest in West and North Vancouver Island (–26.9 and –25.8%) followed by East Vancouver Island (–26.5 and –24.0%; Table 3).

DISCUSSION

We used GIS and habitat suitability modelling to derive estimates of potential marbled murrelet habitat, habitat loss due to harvest and fire, and net change of potential marbled murrelet habitat from 1978 to 2008, which included estimates of habitat recruitment.

Our modelled 2008 estimates of potentially suitable habitat for nesting marbled murrelets in British Columbia were similar to other range-wide binary habitat suitability studies (e.g. Mather et al. 2010). In particular, our estimate of overall 2008 Model 2 potential nesting habitat (2 109 938 ha) was very close to an estimate from an earlier modelling study that used the same parameter set, but some different data sources and methods (1 980 846 ha; Mather et al. 2010). The minor differences in the 2 estimates are most likely due to the data sources; for example, we used Landsat-based change data as opposed to forest inventory data for most of the coast to estimate disturbance (Mather et al. 2010). However, the ~6% difference in the 2 potential habitat availability estimates was largely due to different estimates for the Haida Gwaii and West and North Vancouver Island conservation regions, with our predicted estimates much higher for these regions (Mather et al. 2010, present study). These differences may result from specific variations in model implementation for these 2 regions, as Mather et al. (2010) substituted their coast-wide algorithm with a local model in the Clayoquot Sound area of West Vancouver Island (Bahn & Newsom 2002) and aerial photo interpretation data in Haida Gwaii (Waterhouse et al. 2009, 2010, Burger et al. 2009).

Forest disturbances had the largest impact on Model 2 potential habitat (20.6% loss). Considering the coast-wide scale of the analysis, the estimates of habitat loss were relatively similar across all 3 models. However, estimates of modelled habitat recruitment, and resulting net change in available habitat, varied considerably among models (Table 3). The high level of estimated habitat recruitment in Model 1 is most likely an artefact of the limitations of the forest inventory data (Waterhouse et al. 2010), in conjunction with the most exclusive definition of potentially suitable nesting habitat (CMMRT 2003). In mature forests, age class midpoints were frequently adopted due to difficulty interpreting exact ages, leading to clustering in the for-

est age class frequency distribution (Wong et al. 2003). The high levels of recruitment in Model 1 are likely an artefact of an age class cluster going from <250 yr in 1978 to ≥250 yr in 2008, as opposed to an actual estimate of biologically meaningful nesting habitat recruitment (CMMRT 2003). In general, any estimate of recruitment of potential marbled murrelet nesting habitat over relatively short time scales (e.g. 30 yr) should be considered with caution, as the attributes that 'recruit' through time (e.g. forest age) are simply surrogates based on limited datasets (Waterhouse et al. 2010). In the case of potential marbled murrelet nesting habitat, it is unlikely that the platform characteristics associated with older forests and necessary for marbled murrelet nesting, such as moss-covered branches, 'recruit' within relatively short time frames (CMMRT 2003, Burger et al. 2010). However, this same caution should be applied to single time-frame habitat models, such as our 1978 models. In this case, habitat was deemed suitable by forest stand age or height class; however, some of the identified stands are unlikely to contain the necessary platform characteristics (e.g. forest stand age 251 yr). Thus, excluding considerations of 'recruitment' habitat in the latter time span of change analyses only could lead to a biased interpretation of habitat loss or change.

Our detection of forest disturbances from harvest and fires was limited by the availability of spatial data sets. For example, our forest disturbance data capture only clear-cut type harvesting. Other harvesting practices, such as partial-retention harvesting, can similarly impact potential murrelet nesting habitat. However, throughout our study area the amount of partial-retention type harvesting is relatively small when compared to the level of clear-cut harvest (British Columbia Ministry of Forests and Range 2010). Forest harvests of <1 ha were not captured within 2 of the forest disturbance change layers (our Landsat-based layer, and the change detection layer, Table 2). Complete spatial harvest data for 1978 to 1985 were also lacking (see 'Materials and methods'). To investigate the effect of limited spatial data from 1978 to 1985, we can compare our spatial forest disturbance data with aspatial harvest reporting records in the Ministry of Forests and Range's Annual Reports (British Columbia Ministry of Forests 1979–1986). Our spatial estimates of forest disturbance from 1985 to 2008 (where our data are most complete) align well with documented aspatial harvesting records, suggesting that our disturbance layer is relatively robust and that the missing <1 ha disturbances may be negligible relative to the scale of this analysis.

Given the known deficiency in our data from 1978 to 1985, an option for mitigating this effect is to supplement our estimates using aspatial harvest information

from the annual reports. For example, the total area harvested over our study region from 1978 to 1985, according to the annual reports, was approximately 366 000 ha. This number was generated by adding harvest records from the Vancouver Forest region and the Prince Rupert Forest region, with totals for the Prince Rupert Forest region scaled by 0.44 to reflect the proportion of our study area that fell within this forest region, and assumes no spatial bias of harvests in this region. Using the spatial forest harvest data for 1978 to 1985 (Table 2), 176 000 ha of harvest were spatially detected during this time period and thus already considered in our spatial analyses. Therefore, an additional 190 000 ha of forest loss due to harvest occurred from 1978 to 1985 that we did not detect because of limited spatial data over this time frame. If we assume the same disturbance proportions for the 190 000 ha forest disturbances within each habitat model as other disturbances (Model 1: 26%, Model 2: 50%, Model 3: 73%; see 'Results'), then our adjusted estimates of potential nesting habitat loss would be 19 to 24%, depending on model, or -9 to -22% net change in potential nesting habitat if modelled recruitment is considered. These adjusted estimates are likely closer to the actual degree of potential marbled murrelet nesting habitat loss, although this type of aspatial adjustment includes numerous assumptions.

Our results are based on a set of potential marbled murrelet nesting habitat models, ranging from exclusive to inclusive definitions of potential nesting habitat; however, all 3 models applied are appropriate for broad-scale and strategic planning (e.g. Burger et al. 2005, Mather et al. 2010, Waterhouse et al. 2010). Model 2, which is based on the intermediate parameter set of Mather et al. (2010), performed well in the North Coast conservation region when tested against low-level aerial habitat surveys, with 99% of sites (84/85) modelled as habitat containing some marbled murrelet habitat attributes (Burger et al. 2005). However, Model 2 was found to underestimate habitat suitability when compared to aerial photo assessment methods in other regions of the coast (Waterhouse et al. 2010). The model of Mather et al. (2010) has been selected by the CMMRT as the baseline for monitoring the relative abundance of potential marbled murrelet nesting habitat in British Columbia through time.

Our 30 yr, province-wide spatial analyses and corrected estimates of potential marbled murrelet habitat loss, based on Model 2 (20.6 and 24%, respectively) and Model 3 (16.3 and 20%, respectively), were similar to values reported in previous regional or shorter time-frame analyses of marbled murrelet nesting habitat change in British Columbia. The British Columbia Ministry of Forests estimated that approximately 24% of potential marbled murrelet nesting habitat had been

harvested from 1973 to 2000, based on BTM data (M. Eng pers. comm.). M. Tomlins & M. Gray (unpubl.) reported an 18.3% loss of potential marbled murrelet nesting habitat from 1985 to 2005 in the Sunshine Coast Forest District of British Columbia, with a 12% net loss, when offsetting for recruitment of nesting habitat over the same time period is considered. Finally, the Gowgaia Institute (2007) estimated that 92 776 ha (31 474 ha from 1978 to 1985; 61 302 ha from 1985 to 2008) of forests were logged on Haida Gwaii from 1978 to 2008, based on their high spatial-temporal resolution harvest dataset for the region. Our spatial analysis revealed forest disturbance for Haida Gwaii covering 67 203 ha (9183 ha from 1978 to 1985; 58 020 ha from 1985 to 2008). While our forest disturbance data underestimate disturbance area when compared to high-resolution imagery, the majority of the underestimation occurred expectedly between 1978 and 1985, due to missing spatial harvest records. However, we adjusted for the missing spatial data coast-wide by using an aspatial estimate of additional forest disturbance from 1978 and 1985. Our adjusted coast-wide estimate is likely more robust, regardless of model choice.

Our estimates of potential murrelet habitat and subsequent habitat loss and change are influenced by uncertainty (e.g. upward or downward biases), such as actual suitability of forest stands for breeding murrelets (e.g. presence of suitable limbs for nesting) and known deficiencies in the forest harvest spatial datasets. In our study, Models 2 and 3 produced similar estimates of potential nesting habitat loss and change, and we feel that these 2 models and associated analyses provide a realistic range of potential habitat loss and net change scenarios in British Columbia over the past 30 yr. These results provide the first province-wide habitat change scenarios and are consistent with previous regional analyses of potential marbled murrelet habitat loss in British Columbia.

CONCLUSIONS

Based on our intermediate and inclusive habitat models, with the aspatial adjustment included, we estimate that 20 to 24% of potential marbled murrelet nesting habitat has been lost to forest harvest and fire from 1978 to 2008. If modelled recruitment is considered, then net change in potential nesting habitat would be 20 to 22% loss. The potential marbled murrelet nesting habitat models and our resulting disturbance and change estimates presented here are intended to support strategic land use decisions and monitoring of the status of this wide-ranging species (CMMRT 2003, Steventon et al. 2003, Burger & Water-

house 2009, Waterhouse et al. 2010). Given the paucity of data on population trends of marbled murrelets in British Columbia, these 30 yr changes in terrestrial habitat data are particularly informative for re-occurring assessments of the conservation status of this high-profile species in Canada (COSEWIC 2000).

Broad- and regional-scale modelling of habitat is important for management and provides an approach for monitoring wildlife when population and occurrence data are unavailable (e.g. Berland et al. 2008, Mather et al. 2010, Waterhouse et al. 2010). As with all large-area models, we recommend using our results for strategic planning, and suggest using finer-scaled data products, such as aerial photo interpretation habitat inventories (e.g. Waterhouse et al. 2008, Burger et al. 2009), for tactical planning (e.g. placement of protection or management guidelines, Waterhouse et al. 2010). For future work on coast-wide assessments of potential marbled murrelet habitat changes, we suggest that a closer examination of the spatial patterns of change and loss in nesting habitat (e.g. edges, patch size, and connectivity) may be valuable, as harvesting may actually impact the suitability of nesting habitat in the surrounding intact forest (e.g. Burger 2002, Piatt et al. 2007, Malt & Lank 2007, 2009).

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