A large-scale model for the at-sea distribution and abundance of Marbled Murrelets (*Brachyramphus marmoratus*) during the breeding season in coastal British Columbia, Canada

P.P.W. Yen [a,*,1], F. Huettmann [b,2], F. Cooke [c,3]

[a] *Department of Biological Sciences, Centre for Wildlife Ecology, Simon Fraser University, 8888 University Drive, Burnaby, BC, Canada V5A 1S6*
[b] *Biology and Wildlife Department, Institute of Archic Biology, University of Alaska, Fairbanks, AK 99775, USA*
[c] *Larkin's Cottage, 6 Lynn Road, Castle Rising, Norfolk PE31 6AB, UK*

Abstract

The role that the marine environment plays in the distribution and abundance of Marbled Murrelets (*Brachyramphus marmoratus*), a seabird which nests in old-growth forests, is not well understood. Therefore, we investigated how Marbled Murrelet marine distribution and abundance is related to the abiotic and biotic components of the marine environment. Data on the marine distribution of Marbled Murrelets in British Columbia (BC), densities (birds/km^2; 1972–1993), counts (number of birds per survey; 1922–1989), and pertinent environmental variables as identified from the literature were compiled and then organized in a Geographic Information System (GIS). On a 10 km scale, count surveys were not correlated with density surveys ($r^2 = 0.01$, $P = 0.46$). This suggests the interpretation of count survey data (relative abundance) should be done with care; and it is not further used in this study.

We built a parsimonious model to explain marine densities with marine predictors. First, significant predictors were identified with multivariate Generalized Linear Models (GLMs) by evaluating the shortest distances from survey locations to predictor variables. Murrelet density is higher close to sandy substrate, estuaries and cooler sea temperatures, and lower close to glaciers and herring spawn areas. Model predictors selected by using *P*-values and AIC include sea surface temperature, herring spawn index, estuary locations, distribution of sand and fine gravel substrates (as a proxy for sand lance distribution), and proximity to glaciers. Secondly, spatially explicit large-scale distribution model algorithms use this set of significant predictors to predict Marbled Murrelet abundance (density), distribution and populations in coastal BC. The modelling algorithms used include GLM, Classification and Regression Trees (CART) [Classification and Regression Trees, Wadsworth & Brooks, Pacific Grove, CA, 368 pp.; Software CART and MARS, San Diego, CA] and Tree (SPLUS) [Modern Applied Statistics with S-Plus, Statistics and Computing, 2nd ed., Springer, New York, 462 pp.], Multivariate Adaptive Regression Splines (MARS) [Software CART and MARS, San Diego, CA], and Artificial Neural Networks (ANNs) (SPLUS) [Modern Applied Statistics with S-Plus, Statistics and Computing, 2nd ed., Springer, New York 462 pp.]. Model performances were evaluated by backfitting, and by standardizing models. Tree-SPLUS was identified as the best performing model, and therefore used to predict the maximum carrying capacity

* Corresponding author. Present address: Marine Science Program, Point Reyes Bird Observatory, 4990 Shoreline Highway, Stinson Beach, CA 94970, USA. Tel.: +1-415-868-1221x308; fax: +1-415-868-1946.

E-mail addresses: pyen@prbo.org (P.P.W. Yen), fffh@uaf.edu (F. Huettmann), f.cooke@uea.ac.uk (F. Cooke).

[1] Tel.: +1-415-868-1221x308; fax: +1-415-868-1946.
[2] Tel.: +1-907-474-7882x7671; fax: +1-907-474-6716.
[3] Tel.: +1-553-631-076.

of 170,500 birds for the marine habitat of coastal BC. An additional, a posteriori predictor, the shortest distance to old-growth forest, explained much of the remaining residual variance. This model result led us to a hypothesis of how Marbled Murrelet distribution and abundance relates to proximity to old-growth forests, and it makes an initial basic link between the marine and terrestrial aspects of Marbled Murrelet habitat. Our approach presents the first predictive abundance and distribution models applied to Marbled Murrelets on a large scale (British Columbia coast). Our approach is robust, and the statistical algorithms compared here are fully described and are known to perform well. Our findings are crucial for decision making and consider conservation management on a scale pertinent for the habitat protection of this species.
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1. Introduction

The Marbled Murrelet (*Brachyramphus marmoratus*) is an endangered species in North America that has already been studied intensively (for detailed species account see Ralph et al., 1995; Nelson, 1997; Hull, 1999), but its elusiveness leaves significant gaps in many aspects of its biology. Although approximately 45,000–60,000 Marbled Murrelets are thought to exist in British Columbia (BC) (Rodway et al., 1992; Burger, 1995, unpublished data), there is, at present, limited information on where, and in what quantity they can be found at sea during their breeding season. In general, the distribution of seabirds is positively correlated with food availability, safety from predators, presence of conspecifics and/or abundance of safe nest sites. The breeding requirements of seabirds therefore include both terrestrial and marine components (Hunt et al., 1981; Baird, 1990; Carter and Sealy, 1990; Kaiser and Forbes, 1992; Huettmann and Diamond, 2001). Marbled Murrelets are unique seabirds in that old-growth trees are their primary terrestrial nesting habitat (Nelson, 1997; Huettmann et al., in review).

Adults should forage in productive marine habitats for profitable prey to feed high quality prey items to chicks. However, seabirds may vacate an otherwise suitable nesting area if prey populations are scarce or unavailable within their foraging range (e.g. Ensor, 1979; Vermeer et al., 1979; Bourne, 1981; Gaston, 1982; Sutherland, 1982). Thus, their at-sea distribution and abundance during the breeding season should reflect not only suitable nesting habitat but also the temporal and spatial distribution of food sources at sea (Swartzman et al., 1994; Robards et al., 1999). Studies by Sealy (1974, 1975a,b) have shown that breeding and non-breeding birds often aggregate in distinct areas at sea, presumably in response to local food concentrations. These areas are ultimately constrained by the oceanographic factors that influence and localize these supplies. Although Marbled Murrelet distribution varies with coastline topography, river plumes, riptides or other physical features (Carter and Sealy, 1990; Speckman, 1996; Nelson, 1997), they likely feed inshore (300–2000 m from shore; Hull, 1999), in mainly sheltered waters, and usually where sand lance (*Ammodytes hexapterus*) can be found. Presumably, they aggregate in regions of high marine productivity driven by primary production and prey aggregation (Hunt, 1995). Their movements at sea during the breeding season are also extensive, likely ranging beyond 100 km (K. Nelson, personal communication; B. Cousens, personal communication). Paired adults commute to their nest, located up to approximately 75 km inland, once every 24 h during incubation, and can feed their hatchlings up to eight times per day for a period of 27–40 days (Hirsch et al., 1981; Hamer and Cummins, 1991). One might expect their at-sea distribution to be related to their nesting location and to the proximity of productive foraging areas with abundant prey, especially in the nesting period when food demands are greatest (Marks et al., 1995). It has also been contended by Carter and Sealy (1990) that breeding adults may use alternate foraging sites of varying distance from the nest when foraging for chicks rather than for themselves (B. Cousens, personal communication, see also Huettmann et al., 2002 for Marbled Murrelet use of lake as potential stepping stones during foraging flights).

Habitat suitability models (e.g. U.S. Fish and Wildlife Service, 1981; Brennan et al., 1986) can pre-

Table 1

Data sets compiled supported by literature to best represent Marbled Murrelet marine habitat

Data type	Name	Source	Type	Units/type
Survey	Density surveys	Compiled by Yen and Huettmann (unpublished data)	Georeferenced point	Birds/km^2
	Count surveys		Georeferenced point	Number of birds
Abiotic	Tidal current speed	Foreman (1997)	Interpolated surface	m/s
	Sea surface temperature	NOAA (2000)	Interpolated surface	$^\circ$C
	Estuaries	Yen (unpublished data)	Georeferenced point	Latitude/longitude
	Glaciers	BCMELP (1999)	Polygon	
Biotic	Herring spawn	McCarter and Hay (2000)	Georeferenced point	Spawn index
	Sandy shoreline	Yen (unpublished data)	Polyline	km

dict occurrence and frequency of a species over large areas for which habitat attributes have been measured. Such tools can be advantageous when prioritizing habitats for conservation purposes. The aim of this paper is to investigate the marine environmental variables that influence Marbled Murrelet abundance and distribution in BC (48–55°N, 123–133°W) during the breeding season from April to August (including partial pre-breeding, breeding and partial post-breeding period); secondly, we try to predict the spatial distribution and abundance of Marbled Murrelets. In order to achieve this, we compiled the best known available data on Marbled Murrelet distribution throughout British Columbia, and marine environmental variables based on the literature such as current speed, sea surface temperature, proximity to Herring spawning grounds, sandy substrates (preferred by Pacific Sand Lance), and glaciers (Table 1). This approach contrasts with previous modelling techniques that considered only terrestrial habitat (Meyer, 1999; Steventon et al., 2003; V. Bahn, personal communication; D.P. Escene, personal communication). We used as an a posteriori candidate variable a key terrestrial feature, proximity to old-growth forest, to explain the remaining residual variance in the marine model. Proximity to old-growth forest (potential nest locations) is generally believed to be a limiting factor for these birds in the breeding season (Marks et al., 1995). This preliminary analysis allows for an initial comparison and hypothesis of how the marine and terrestrial components correlate with Marbled Murrelet abundance and distribution to be further tested in a forthcoming paper (Huettmann and Yen, unpublished).

Habitat models can be used to extrapolate and fill survey gaps by predicting the spatial marine distri-

bution and abundance of seabirds such as Murrelets (e.g. Huettmann and Diamond, 2001). Therefore, we develop a parsimonious model that best explains the spatial distribution and abundance of Murrelets. We then apply robust prediction algorithms to estimate the abundance and distribution of Marbled Murrelets along the BC coast, within 1 km offshore. Sometimes models are not validated rigorously or perform poorly when tested (Dedon et al., 1986; Raphael and Marcot, 1986; Johnson et al., 1989). Therefore, we evaluate our models on their ability to predict known Marbled Murrelet occurrences. By using a large-scale approach, we hope to demonstrate the importance of providing a broadened picture of Murrelet habitat use to improve our knowledge of this bird with applications for conservation management.

2. Methods

2.1. Survey data

Published data on Marbled Murrelet abundances in British Columbia were compiled for count (relative abundance: number of Murrelets counted per site. Source: Campbell et al., 1990; Kaiser, unpublished data) and density (absolute abundance: birds/km^2. Sources: Burger, 1995; Lougheed, 1999) surveys conducted during the breeding season (April–August). For consistency, we compiled only observations made on the coast (land and boat based), including fjords and bays, and excluded those from inland lakes. These compiled survey data represent the best-known information on Marbled Murrelet marine abundance
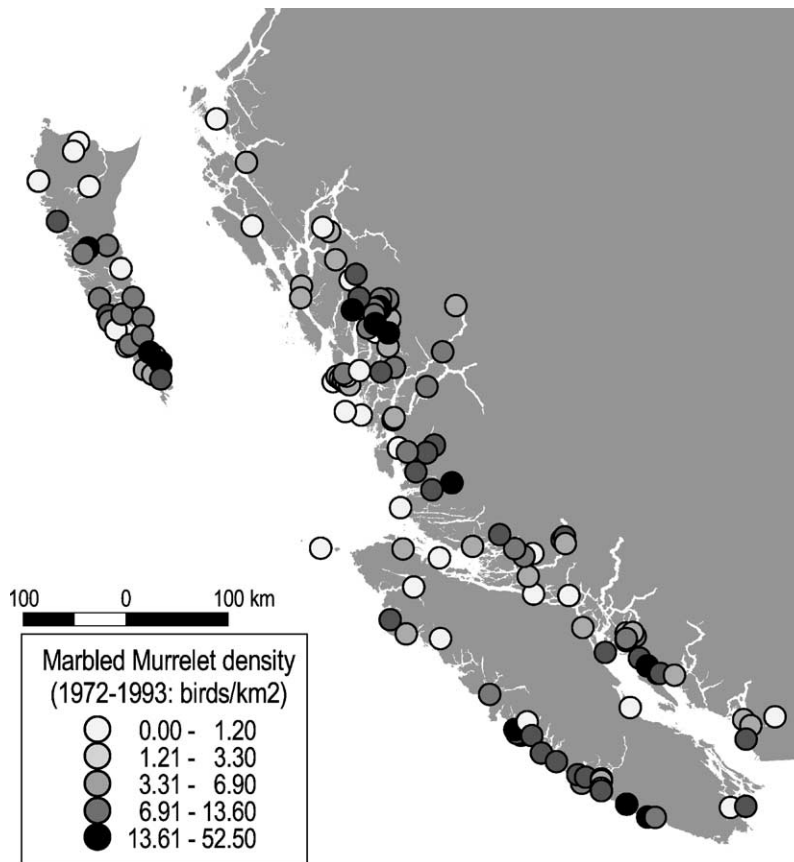
Fig. 1. Map of compiled density data for Marbled Murrelet density (birds/km^2) from 1972 to 1993.

and distribution in British Columbia (density: Fig. 1 and Table 1).

We georeferenced all survey data using BC Geographical Names Information System (http://home.gdbc.gov.bc.ca/) and assembled these in a database (EXCEL and transferred to dBASE); they were displayed with ArcView 3.2 (ESRI, 1996). The count surveys (relative abundance) cover a time period 1922–1989 with the majority of the surveys conducted from late 1960s onwards; the density surveys (absolute abundance) cover a time period 1972–1993. When duplicated surveys at the same location occurred, the averaged survey was used. The two types of surveys, density ($n = 244$ locations surveyed) and counts ($n = 384$ locations surveyed), were generally independent of each other, and each was conducted by different observers. Surveys on 'confirmed absence' were seldom collected and occur only in the density

data set (as zeros). Confirmed absence differs from survey gaps in that this locale has been investigated and no birds were found. Absences potentially represent regions of low oceanographic productivity with adverse effects on Murrelet survival. Due to the unequal survey effort, counting efforts and differing counting protocols, these count and density surveys should still be considered approximate indices of Murrelet abundance along the relatively inaccessible coastline of British Columbia. However, density surveys are a more standardized representation of abundance than are count surveys, since counts (index of relative abundance) do not take into account the area surveyed (e.g. Buckland et al., 1993). This is reflected in our data sets in that on a 10 km scale and corrected for coastline length we detected no correlation between the count and density surveys ($r^2 = 0.01$, $P = 0.46$; despite the suggestion by Newton, 1996

that such a correlation may exist). For this reason, we regarded the count survey data as too unreliable for analysis and thus excluded from further investigations.

2.2. Abiotic environmental data

We compiled Geographic Information System (GIS) data sets to investigate and describe the productivity of the marine environment within the study area. The environmental features (Table 1) were selected based on existing knowledge of Marbled Murrelets' ecological requirements. All data used apply to the Marbled Murrelet breeding season (April–August; Table 1).

Data on tidal current (cm/s) were generated from a three-dimensional predictive model constructed by Foreman and Henry (1993) and Foreman et al. (1995). This model has been tested in the field, was found to be very reliable and forms the basis for tide table calculations and marine navigation applications (Foreman and Thomson, 1997).

Information on 'sea surface temperature' was obtained from the National Oceanic and Atmospheric Administration (NOAA Coastwatch, 2000) website as point data (for methods see also Huettmann and Diamond, 2001). It consists of monthly long-term temperature averages, with a spatial resolution of a 1° of latitude by 1° of longitude grid cell. The average sea surface temperature from April to August was used to describe the sea temperature of the study area. The point data were smoothed as an interpolated surface by creating a contour using the inverse distance weighted (IDW) method in ArcView.

Fjords that receive glacial run-offs have enhanced marine productivity (e.g. Dunbar, 1973; Shaw, 1989) and thus could attract Murrelets. Glaciers of BC are mapped and available in GIS format from the BC Watershed Atlas (Ministry of Environment Land and Parks, 1999). This GIS data presents known glaciers, as identifiable from satellite images (Fig. 2a).

Estuary locations are also important where river discharge mixes with seawater. This mechanism has been known to increase primary production (Yin et al., 1997), but visibility could be affected for underwater foraging birds. In some cases, the productivity occurs at the frontal zones that form when river and tidal flow are in opposition (Dustan and Pinckney, 1989). Estuary locations are derived from the BC Watershed Atlas: 'Watershed Group Rivers, Lakes, Wetlands and
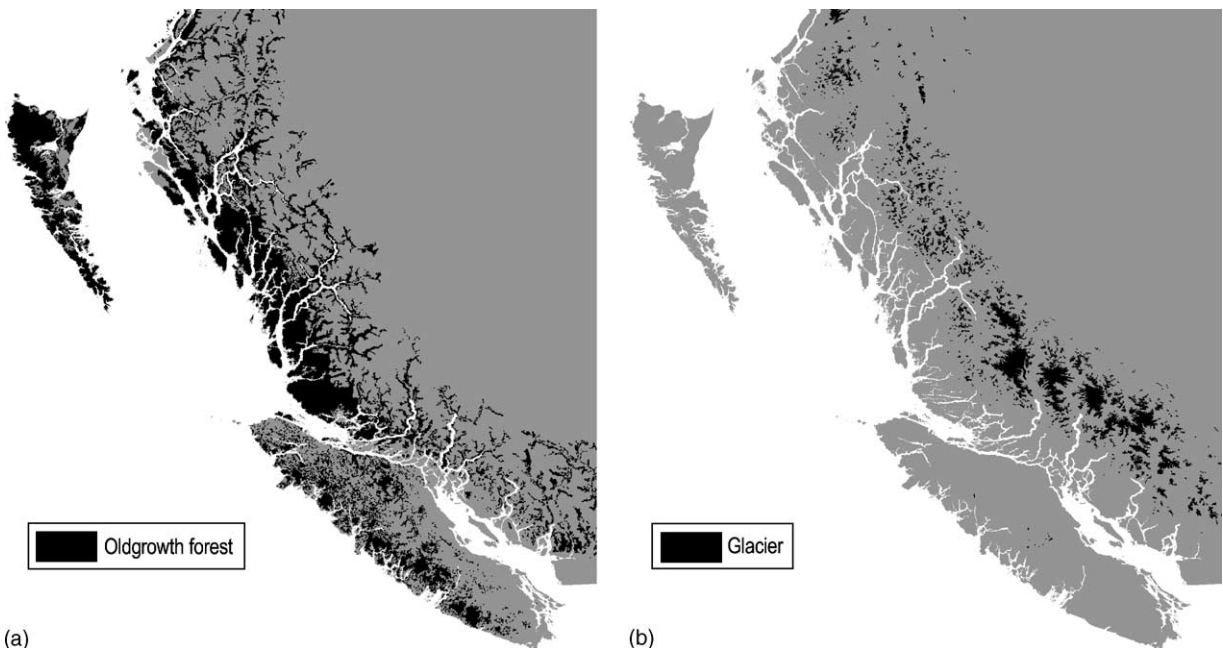

Fig. 2. Maps of (a) known glaciers and (b) known old-growth forest distribution in British Columbia (Inforain, 1998; Ministry of Environment Land and Parks, 1999).

Man-made Waterbodies Layer' at the 1:50,000 scale (Ministry of Environment Land and Parks, 1999). The estuary location was determined from where the river polyline meets the coastline.

2.3. Biotic data

Details for biotic data are shown in Table 1. Data on herring spawn distribution were obtained from the Cumulative Herring Spawning Index (Hay and McCarter, 1999). The Cumulative Spawn Habitat Index is used as a measure of habitat suitability for herring, as it takes into account both the frequency and magnitude of recorded spawns. This index is derived from the product of the length of spawning area (m) and the estimate of median egg thickness layers and median width, determined for each surveyed spawning location (Hay and McCarter, 1999). The spatial distribution of the spawn events was organized by a 'shoreline kilometer system' where the geographical positions of each spawning event in 0.1 km segments were estimated along the shoreline (for further details see Hay and McCarter, 1999). This data set was further partitioned into separate data layers using their five quantiles. The top, and lowest quantiles, were then extracted and established as separate themes, to be further used for the models. The top and lowest quantiles were used since they represent the extreme values that are likely to be most influential for Murrelet distribution.

Sand lance are another key food item in the marine food chain (Wilson et al., 1999); and may act as an indicator for marine productivity. They comprise a major portion of Marbled Murrelet diet (Hobson, 1990; Burkett, 1995), especially during the spring and summer feeding periods when most sand lance grow and gain weight (Kitakata, 1957; Blackburn and Anderson, 1997). Because consistent data on Sand lance abundance have not been collected for coastal British Columbia, we relied on the location and length of sandy shorelines as an indicator of Sand lance presence. Sand lance alternate between lying buried in soft wet sand (Girsa and Danilov, 1976; Pearson et al., 1984; Pinto et al., 1984) and swimming in open waters in schools (Inoue et al., 1967; Dick and Warner, 1982). Hence, they are typically associated with fine gravel and sandy substrates including the intertidal zones (O'Connell and Fives, 1995). The

substrate data are a combination of two data sources. The first was obtained from the West Coast offshore environment map from Department of Fisheries and Environment (1978) and was digitized by hand. The second is the digital sandy shoreline layer from Baseline Thematic Mapping (Ministry of Environment Land and Parks, 1999).

2.4. Old-growth forest data

The marine distribution of Marbled Murrelets may be constrained by a terrestrial variable, the amount of old-growth forest nearby that is available for nesting habitat (e.g. Marks et al., 1995). In the absence of consistent old-growth forest inventory maps for British Columbia, we used a data set (Inforain, 1998) available from the internet/WWW (Fig. 2b). These data were not included in the predictive model, but will be used in an a posteriori model evaluation.

2.5. Data sets not used in this study

Although plankton is a major trophic component of the marine food web, no plankton data were found that would cover our study area in its entirety and that had been collected consistently. Pelagic (here defined as >5 km from shore) Marbled Murrelet survey data were also not included, since our interest lies in coastal interactions alone. Although pelagic seabird datasets were not available to us, no major pelagic Marbled Murrelet sightings are known in British Columbia during the breeding season (Morgan et al., 1991; Morgan, personal communication).

2.6. GIS and data query

For data presentation, manipulation and analysis, we used ArcView 3.2, in an IBM PC operating system. All our data were projected into the standard Albers projection of British Columbia (for details contact authors).

Reference points used to apply the predictive model were added along the BC coastline, including Vancouver Island and the Queen Charlotte Islands, of approximately 37,000 km total length. 2100 points were placed 10 km apart on a mapping unit of 1:2 million scale using the Script 'Divide line by adding points evenly', obtainable from the WWW

(http://gis.esri.com/arcscripts/). We measured the distance in meters from every point (evenly spaced and surveyed points) to the nearest feature for some environmental themes (glacier, sandy substrate, estuaries), and prey type theme (herring spawn). This was done in ArcView, using the Script 'Nearest Features v. 3', downloadable from the ESRI internet/WWW (http://gis.esri.com/arcscripts/). For the same points, sea surface temperature and tidal current speed overlays were extracted.

2.7. Multivariate model construction

For selecting the model predictors, we used a Generalized Linear Model (GLM), family = Poisson, link = log. In general, we followed the approaches described by Preisler et al. (1997) and Huettmann and Diamond (2001). Poisson distribution was used due to the right-skewed distribution of the density survey data (Preisler et al., 1997). Our parsimonious model included predictors that had a correlation with each other of less than 0.4. We used chi-squared ANOVA (order-dependent) to obtain *P*-values, and a null model to obtain C_p values (quasi AIC, more or less order-independent) for an alternative evaluation of the predictors (Venables and Ripley, 1994, 2002; Burnham and Anderson, 1999, 2002; StatSci, 2000). The predictor that explained more of the deviance of the pair replaced pairs of predictors correlated above the threshold, 0.4. This method reduces correlation within the model and selects the most predictive variable. Significant predictors for the parsimonious model were also evaluated by AIC allowing for a sound model inference (Burnham and Anderson, 1999, 2002).

In order to fill the gaps on Marbled Murrelet abundance and distribution due to unequal or missing survey efforts, we applied additional modelling algorithms known for their strength of fitting and predictive power for wildlife distribution data (e.g. Verner et al., 1986; Huettmann and Diamond, 2001; Scott et al., 2002). The algorithms used besides GLM (Venables and Ripley, 1994, 2002; Meyer, 1999) are Classification and Regression Tree (CART from Breiman et al., 1984; Bell, 1996; O'Connor and Jones, 1997; Steinberg and Colla, 1997; Salford Systems, 2001), Tree from SPLUS (Venables and Ripley, 1994; StatSci, 2000; Huettmann and Diamond, 2001), Mul-

tiple Adaptive Regression Splines (MARS; Friedman, 1991; Steinberg et al., 1999; Salford Systems, 2001), and Artificial Neural Networks (ANNs, Venables and Ripley, 1994; Scardi, 1996; Özesmi and Özesmi, 1999; StatSci, 2000). Except for the GLM, all models used non-linear approaches to fit the data. These algorithms are well described, robust, and were already used in wildlife modelling applications; further details can be found in references given (O'Connor, 2000; Hastie et al., 2001).

Classification and Regression Trees (CART) starts with the parent nodes and uses the method of binary recursive partitioning; the nodes are split subsequentially into two child nodes following a maximized split criterion (Breiman et al., 1984). This process is then repeated as the child nodes are treated as parent nodes and split again until further splitting is not possible or is stopped and terminal nodes remain. Cross-validation can be used to report an estimate of the predictive accuracy of the tree by removing a part of the data to construct the tree and using the removed data as the test sample to obtain the error rate. This process is repeated multiple times on each occasion removing a different portion of the data until a reliable error can then be applied to the tree (Hastie et al., 2001). For our distribution and abundance model, we used CART default settings and combined 15 trees to obtain a stable model. For Tree-SPLUS, we also used default settings, no node pruning, a minimum node size of 2 and a 'response' type for prediction.

Multivariate adaptive regression splines (MARS) developed by Friedman (1991) are a kind of additive model (Hastie and Tibshirani, 1986) that can be seen as a generalization of regression trees. It is a multivariate non-parametric regression procedure that fits splines to distinct intervals of the predictor variable to build powerful regression models (Hastie et al., 2001). Two steps are involved in model construction; first, the procedure produces an overfit model and the second step works to eliminate redundant factors and components that contribute the least to the model. In our MARS model, we selected for 100 interactions in basis functions, with six maximum interactions and a 12-fold cross validation.

Artificial Neural Networks (ANNs) are electronic networks of 'neurons' that process and 'learn' by comparing the classification of data records individually (Ripley, 1996; Lek and Guegan, 1999; Özesmi and

Özesmi, 1999). The errors from the initial classification of the first record is fed back into the network, and used to modify the networks algorithm in the next round, and so on for repeated iterations. The network consists of several layers of neurons, an input layer, hidden layers, and output layers. Input layers take the input and distribute it to the hidden layers (the user cannot see the inputs or outputs for those layers). These hidden layers are required for all necessary computations and transfer the results to the output layer (Hastie et al., 2001). Our ANN model used 0 decay, 4 hidden units, enabled layer skipping and a 'raw' type prediction.

Overall, we followed general default settings of the non-linear algorithms used to allow for algorithm comparisons without special 'tuning'. Our approach using first a GLM for predictor selection followed by non-linear algorithms modelling does not allow for a valid comparison of the importance weighting for predictors across all algorithms; thus, we did not further report this metric.

The predictive models are utilized in two ways. First, they are applied to the habitat features of the evenly spaced points to predict a coastal distribution and abundance of Marbled Murrelets. Next, the models were tested by reapplying each model on the input data for which the Murrelet density is already available (backfitting). The observed abundance was subtracted from the predicted abundance for each survey case. An evaluation of the model performance was based on the distribution of the obtained error. Aside from traditional backfitting, we converted the predicted densities to a percentage of the total sum of predicted density in order to obtain a second, standardized measure of model performance across all predictive algorithms used. Thus, we know the proportion of the total predicted birds and which occur at specific locations. Based on the predicted abundance and distribution of Marbled Murrelets in coastal British Columbia (defined as 1 km offshore), we can extrapolate an estimate of the overall population for BC. Because our model extrapolates densities (birds/km^2) to one location every 10 km interval coastline, we multiplied the predicted densities by 10 to obtain populations within 1 km distance off the coast (see also Hedley, 2000).

To evaluate the findings from the predictions for the marine habitat a posteriori, we applied an external dataset, amount of old-growth forest, to the predictions of even points, and measured the nearest distances. This allows us to explain the remaining 'noise', prediction residuals, from the GLM by the suggested link with Murrelets' known principal terrestrial habitat (Marks et al., 1995; Ralph et al., 1995; Nelson, 1997). This terrestrial dataset plays a considerable role in the overall Murrelet distribution (Ralph et al., 1995). It is not included in the model since the purpose of the model is to determine the effects of marine productivity alone on Murrelet breeding distribution. This approach still allows us to draw a preliminary association between Murrelet's overall habitat requirements (marine and terrestrial).

3. Results

3.1. Compiled surveys

The general Marbled Murrelet abundance and distribution patterns pooled for BC over the years 1930–1996 is shown in Fig. 1. Fig. 3 describes bird abundance and distribution by latitude; Marbled Murrelets were found in abundance along the entire BC coast (density: average (S.D.); 7.24 (6.57) birds/km^2), with major concentrations between 52 and 53°N. However, apparent gaps, particularly on the northern mainland coast, may be attributed to shortage of survey effort rather than lack of birds. We pooled data across years, because we detected no consistent patterns within years. This may be due to averaging affects when working with large geographical scales. In contrast to findings by Burger (1999), we detected no El Nino year effects, and conclude that either our data were unable to detect these effects, which may be attributed to inconsistent survey effort across years or data quality, or, that these effects are minor or non-existent (consider also Thomas, 1996, 1997). More studies are needed on this topic.

3.2. GLM

For the parsimonious GLM, we identified estuaries, sea surface temperature, sandy shores, glaciers, and a low value for the herring as the most important predictors of Marbled Murrelet abundance and distribution (Table 2). We also investigated the use of the 'best-fit model', which would achieve a better model fit and
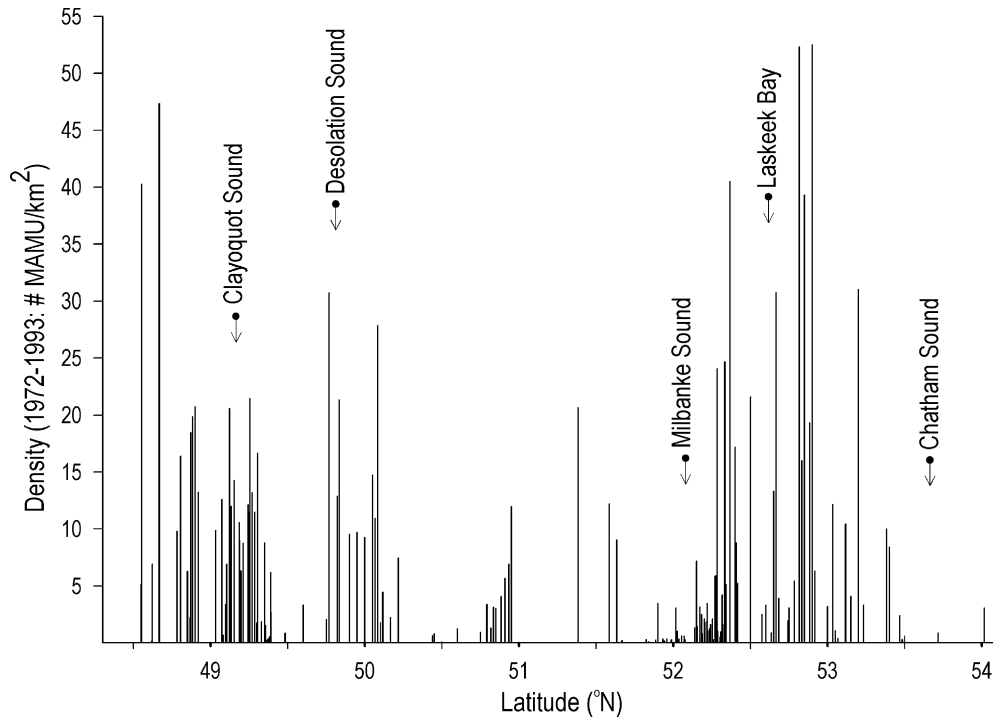
Fig. 3. Count and density surveys pooled over all years by North Latitude.

model predictions by being less parsimonious since it allows for higher correlation among the predictors (non-parsimonious model). However, using this type of model did not improve the amount of residual deviance explained 1965 (best-fit) versus 1966 (parsimonious) of an overall 2315 residual deviance (Table 2). Therefore, this approach was not further pursued. The parsimonious GLM is used to allow for the best inference on the determination of Marbled Murrelet ma-

rine habitat selection (Burnham and Anderson, 1999, 2002).

We found positive correlations between Murrelet density and proximity to estuaries, and sandy substrates, and lower sea surface temperatures. This indicates that Marbled Murrelets show preference for cooler waters and are found closer to estuaries and sandy bottoms. Negative correlations with proximity to glaciers and high herring spawn index were found, suggesting birds prefer to be further from glaciers and away from areas where herring spawn.

3.3. Model evaluations and performances

The backfitting results show that for Tree-SPLUS and CART, the means and the median of the differences between the observed and predicted values are at or close to 0 (Table 3 and Fig. 4). For the other models, the mean lies below the median, signifying a general tendency to overestimate the Murrelet abundance. MARS and ANN models performed similarly; the GLM had the greatest standard deviation (S.D. =

Table 2

Significant predictors in the parsimonious GLM of the density surveys used in the BC coast model ($n = 244$)

Predictors	P-value	C_p	Intercept	Coefficient
Estuary	<0.0001	2969	−0.09	−9.01E−5
Sea surface temperature	<0.0001	2968	−0.98	−4.75E−2
Sandy shores	0.0001	2897	−0.14	−5.03E−6
Glacier	<0.0001	2961	−0.30	1.78E−6
Low Herring	<0.0001	2948	−0.33	1.60E−5

Residual deviance explained of the parsimonious model = 1966 of 2315.

Table 3
British Columbia population estimates (maximum marine carrying capacity) from density models and rounded off to the nearest thousands

	GLM	CART	Tree	MARS	ANNs
Estimated population	176000	179000	170500	183700	164000

All values corrected for backfitting errors.

Table 4
Model evaluation based on the summary of backfitting results from Marbled Murrelet predicted abundances 10 km apart

	ANNs	CART	MARS	Tree	GLM
Mean	0.0	0.0	0.0	0.0	0.0
Median	2.1	0.1	2.5	0.0	2.0
S.D.	8.6	4.6	8.6	2.9	8.8

8.8). The Tree-SPLUS algorithm also better predicted the real density than all other algorithms with a S.D. of 2.9 (Table 4).

Fig. 5 compares the relative algorithm outputs of the predictions. The magnitude of percent of predicted output is expected to be similar across algorithms used. Although Fig. 5 shows that this is not always the case, consistent trends remain on the larger scale. The percentage values of predictions can be seen as an indicator of the quality of the algorithm. In this regard, the Tree-SPLUS algorithm performs best. In addition, the differences among models demonstrate the importance of including different scenarios for the prediction of Marbled Murrelets and not relying on a particular model alone.

Difference between observed and predicted density
○ -43.40 - -3.10
◔ -3.11 - 0.00
◑ 0.01 - 2.50
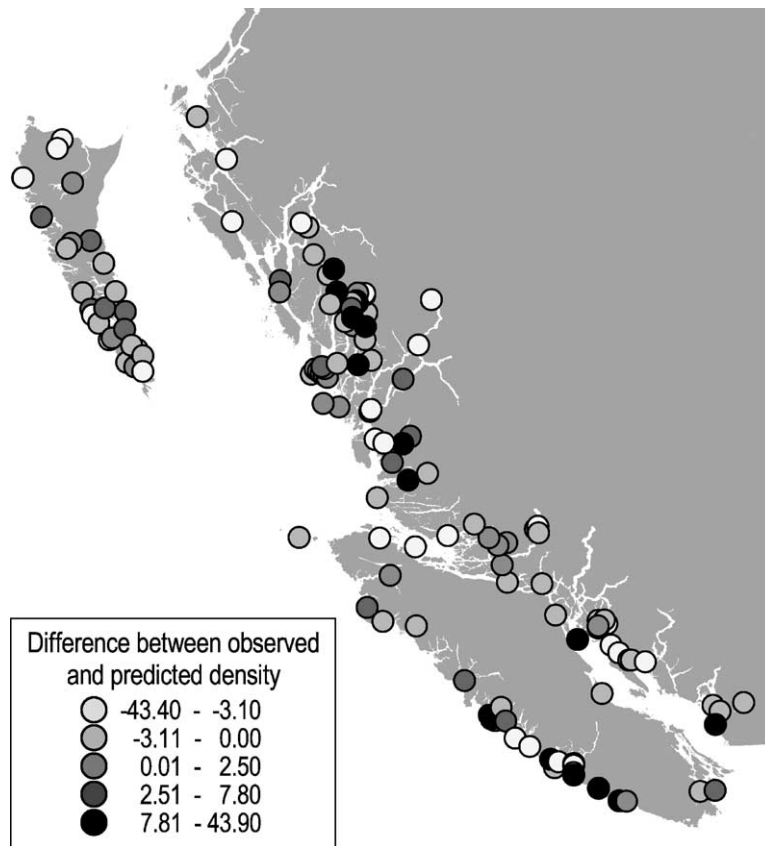◕ 2.51 - 7.80
● 7.81 - 43.90

Fig. 4. The difference in estimates between the observed density and the density predicted by the tree algorithm. The classification is divided into five quantiles.
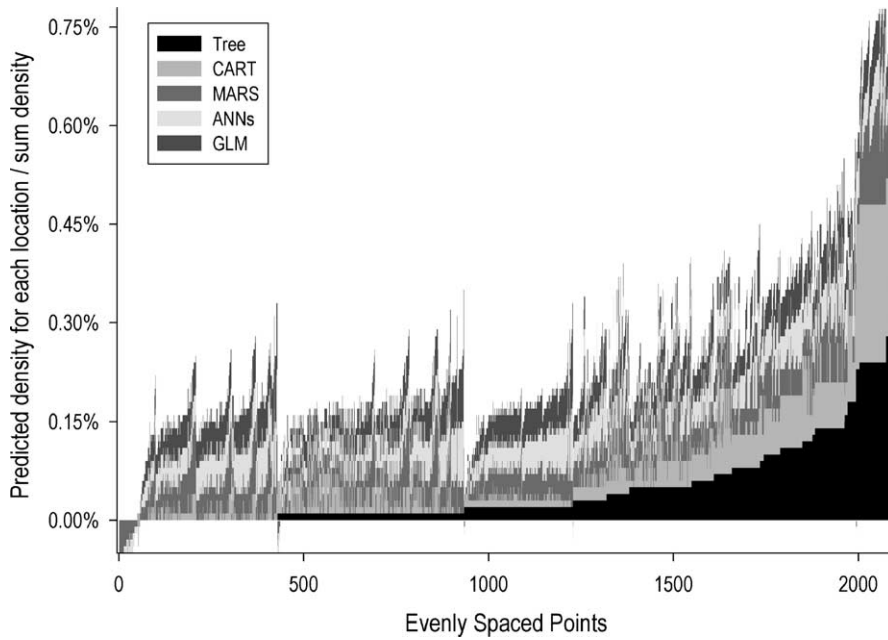
Fig. 5. A visual comparison of all model behaviours at the same locations. Each percent represents individual predictions divided by the sum of the predicted densities across all modelling algorithms used.
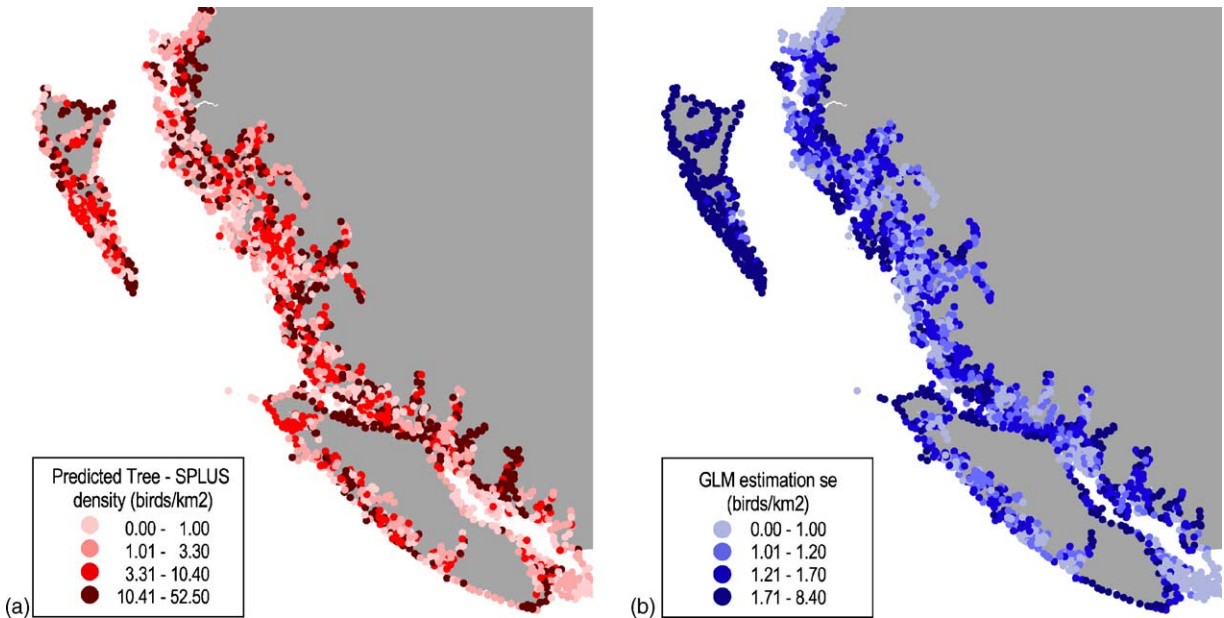

Fig. 6. (a) Predictive Tree model output for Marbled Murrelet densities along the BC coast. (b) The distribution of GLM standard error.

3.4. Predictive map and predicted population estimates

Fig. 6a is based on the classification and regression tree (Tree from SPLUS) model identified as the best model based on criteria used. Besides predictions, we also show the related standard error of the GLM with the selected predictors (Fig. 6b). Doing so allows for evaluation of the spatial prediction accuracy for individual locations. For the predicted density model, the areas Southern and North Eastern Queen Charlotte Island, Discovery Passage, Southern Vancouver Island, the fjords of Central Coast, Southern and Western Vancouver Island and the fjords of Strait of Georgia showed higher abundances. Predicted densities are low north of Queen Charlotte Island, Northern coastal British Columbia, Northern Vancouver Island and Southwest of Vancouver Island.

Results for estimated populations from the used algorithms range from 164,000 to 184,000 with the best prediction from the Tree-SPLUS algorithm with the lowest S.D. (Table 4) of 170,500 birds (Tables 3 and 4). Since our observed density data were collected during 1972–1993, the predicted estimates likely need to be interpreted as the average population size for these years.

3.5. Explaining the remaining variance with terrestrial feature: old-growth forest

Taking into account the hypothesized relation between Marbled Murrelets and old-growth forests, the standard error of the GLM might be explained by the proximity to closest old-growth habitat (Fig. 7). For predicted densities, locations less than 30 km from old-growth forests (regions A and B; Fig. 7), show higher abundances. Region B (Fig. 7) is characterized by the highest densities as well as the highest standard errors. Points beyond 30 km from old-growth forest show very low abundances and have low standard
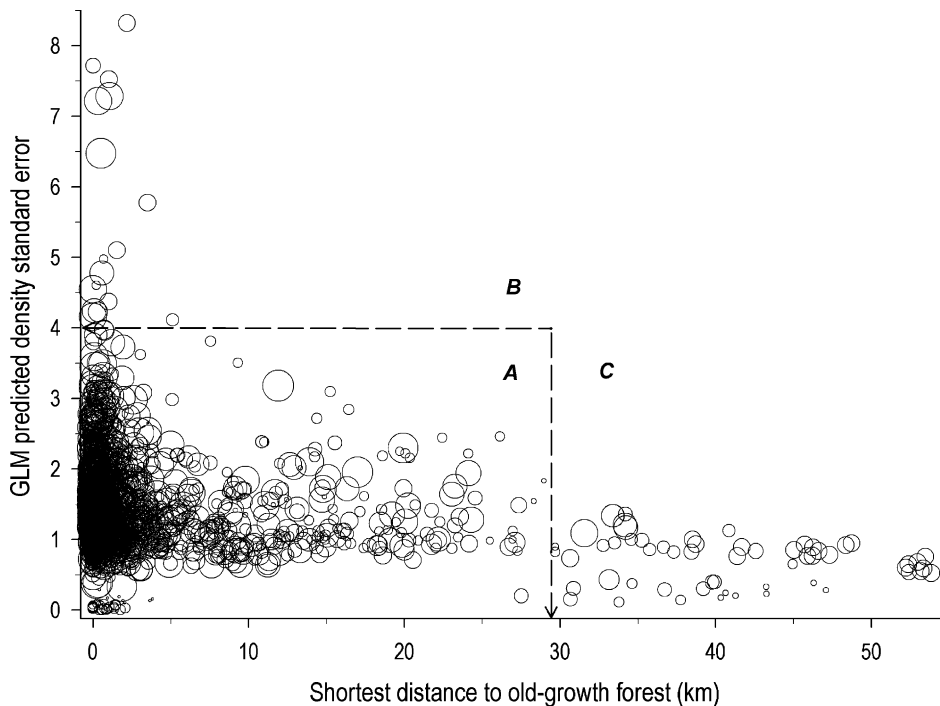

Fig. 7. Evaluation of the model prediction standard error by the nearest distance to old-growth forests. This terrestrial feature is an essential component of Murrelets' nesting habitat and their distribution is likely influenced to some extent by this feature. However, since our model only deals with their marine components, the model prediction standard error likely can be accounted for distance to this feature. The size of each point is determined by the magnitude of the tree predicted density. Therefore, the larger the point, the greater the density.

error (region C; Fig. 7). In general, the variance increases as the distance to old-growth forest decreases below approximately 5 km.

4. Discussion

Large-scale at-sea Marbled Murrelet distribution and abundance patterns can be correlated with abiotic and biotic variables. Our findings demonstrate relations between the Marbled Murrelet's spatial distribution and abiotic and biotic factors. The resultant density models generated from the selected significant variables largely agreed in their predictions of the most and least populated areas. Since only the breeding period is investigated, there is the added complexity of non-breeders, which include failed and pre-breeders. Non-breeders do not have the same distribution constraints as the nesting breeders (Speckman, 1996) and likely will have different distribution patterns as a result. Close proximity to a prime foraging area during breeding will reduce travel costs for adults feeding offspring, and may also enhance the survival of fledglings immediately after leaving the nest. Non-breeders may also benefit from the productive environment, e.g. food or future mating partners.

4.1. Marbled Murrelet surveys, counts and density

Due to the insufficient sample size of absence surveys, a bimodal model (presence/absence; e.g. Huettmann and Diamond, 2001) could not be used; instead, we used a Poisson distribution, as it is commonly applied to survey data for predicting abundance. Nevertheless, a lack of surveys must not be confused with absence data. The importance of recording absence during surveys should be emphasized for its applications in survey-based management applications. Concurrently, high densities are not necessarily an adequate indicator of habitat quality (Van Horne, 1983), but we are unable to correct for this potential effect since all surveys were conducted independent of a unifying protocol reporting how the observed birds really use the marine habitat. In view of the lack of a positive correlation between the count and density surveys, we were not able to perform ground-truthing of the density model with count surveys. Unfortunately, this results in the loss of one step

in the model evaluation process. This also signals that interpretations of count data should be done with care, e.g. regarding distribution and population trends.

Since the birds were widely spread along the BC coastline, it is unlikely that localized catastrophes such as fisheries and oil-spills would potentially affect the entire Canadian Marbled Murrelet population simultaneously, at least not in the breeding season.

4.2. Sand lance

In the absence of consistent large-scale sand lance distribution data for BC, we used sandy bottoms (in waters 0–200 m deep) as a sand lance habitat indicator (Robards et al., 1999). Sand lance may be vital for chick rearing by Marbled Murrelets, as well as other seabirds. This is supported by the tendency for greater numbers to be found closer to sandy substrates. For instance, in the related species, Rhinoceros Auklets (Bertram and Kaiser, 1993), chicks receiving a high proportion of sand lance in their diet, had heavier fledging weights and grew significantly faster than those receiving fewer sand lances (Wilson and Manuwal, 1986; Bertram and Kaiser, 1993). It has been suggested that seabird chick diets and/or growth rates may act as indices of the status of marine fish populations (Cairns, 1987; Croxall et al., 1988; Montevecchi et al., 1989).

4.3. Pacific herring

Vermeer (1992) and Carter (1984) have demonstrated the importance of the Pacific herring in the diet of Murrelets. Along with sand lance, these two species make up the bulk of Murrelet diet during the breeding season. In addition, McGurk and Warburton (1992) found that herring and sand lance larvae consumed prey of similar lengths and width. They concluded that herring and sand lance larvae compete for the same prey resource, mainly copepods (subclass: Copepoda). Thus, it may be concluded that their populations are affected by similar environmental parameters that influence their prey presence.

In recent years, the number of spawning records appears to have declined in almost all areas of BC while the volume of spawn has increased (Hay and McCarter, 1999). Although the reasons are not known and may be due to a decrease of survey and search

effort, this could have far-reaching effects for Murrelets and other seabirds that rely on herring as a food source. Little has been done to quantify the effects, if any, of commercial herring harvesting on Murrelets' abundance and reproductive success.

Recently, there has been an increasing awareness of nearshore developments, such as 'log booming' activities, and mariculture establishments which could affect water quality (Hay and McCarter, 1999) and the spawning sites of herring. In addition, the large-scale impacts of oil spills, fisheries and ocean climate changes on herring spawn distribution should also be considered as detrimental to Murrelet populations.

4.4. Glaciers and estuaries

Glaciers and estuaries have certain features in common. They both result in an influx of fresh water and both lead to mixing of water bodies, yet estuaries are positively correlated with Murrelet density, whereas glaciers are negatively correlated.

We found that Murrelets tend to be found further from glaciers. This provides a new aspect of stratifying the marine environment relevant to Marbled Murrelets. The further the distance from glaciers, the less likely Marbled Murrelets will encounter run-off formed by glacial meltwater (Dunbar, 1973; Matthews and Quinlan, 1975).

Estuaries are unique aquatic environments that have an additional source of buoyancy input derived from freshwater inflow, and an additional source of mechanical energy from tidal stirring. As a consequence of a combination of estuary surroundings without glacial meltwater, distinct bloom dynamics can be established that are different from those observed in lakes and open oceans (see also Cloern, 1991).

The mechanics of this mixing are initiated when the discharged water mixes with the saltwater, and plume fronts often form. This mixing may take place in an estuary, or directly in the open ocean where the estuary itself discharges into the coastal sea. Due to differences in salinity and temperature, a distinct front can form that will support high biological activity. Following the nutrient enhancement from the meltwater, this region of front will produce high plankton growth (Revelante and Gilmartin, 1976). It is currently not well understood whether sediment from the mixing can affect visibility and foraging of Marbled

Murrelets, however our finding supports an avoidance of water with glacial run-off characterized by reduced visibility from siltation (Speckman et al., 2000).

4.5. Sea surface temperature

In the past, there has been a widespread consensus that marine populations respond to climatic events, such as ENSO (Burger, 1999). Sea surface temperature is a relatively well-sampled measure that can be used to interpret large-scale climatic variability. Temperature variations not only affect an organism's metabolic rate directly but also influence other biotic variables such as local current and thus plankton movement (McGowan et al., 1998). It is uncertain whether sea surface temperature is a reliable indicator for the actual water body as such, particularly in stratified waters. An association can be made in this case, since Marbled Murrelets are known to feed at the surface (Carter and Sealy, 1982; Nelson, 1997). Our findings agree with past research indicating that Marbled Murrelets avoid waters with high sea surface temperature (Burger, 1999; Lougheed, 1999).

4.6. Multivariate modelling

Modelling species distribution and abundance using GIS and multivariate statistics is emerging and linked to the increasing availability and quality of computing tools (Verner et al., 1986) and large volumes of georeferenced data. Good models increase their accuracy and scale with increasing data quality and availability, and with robust model methodology. However, there is a trade-off between the benefit of a model, and the quality of input data: the higher the quality and coverage (spatial and temporal) of the survey data, the less the need for a spatial predictive model. Normally, models are presented as successive versions of 'model generations', each replaced by an improved model when better tools and data become available. The selection of predictors for such models and the inference needs careful consideration in any modelling approach (Burnham and Anderson, 1999). Although all of our models generated by robust algorithms use the same set of predictors, the predicted responses differed slightly (Fig. 5, Tables 3 and 4). This may be due to the input data having a high error, specific model algorithm settings, or perhaps also that an investigation

of a more detailed distribution scenario for Marbled Murrelets is needed (e.g. finer spatial and temporal stratification).

To fit the response variables, Poisson distribution, logit GLM was used. Our density data fit the Poisson distribution well, as visually inspected. Although the response variable (density survey) was unlikely completely random, the results are still reliable due to the robust GLM method (Preisler et al., 1997) and to a large sample size. Using a GLM to select the suitable predictors in concert with a non-linear model prediction algorithm (Tree-SPLUS) was the approach we believe best fills the existing data gaps for Marbled Murrelet abundance and distribution in BC (see Huettmann and Diamond, 2001). The non-linear algorithms can present a 'black-box' approach (e.g. Hastie et al., 2001), however, they perform quickly and are more convenient than for instance the more traditional GLM method.

4.7. Model performance

The algorithms used to generate our model are statistically well known and are robust (e.g. Hastie et al., 2001), but our findings still should be further evaluated. Because standard errors were not given for most of the cases (CART, MARS, ANNs, Tree), we used backfitting as an alternate method to assess each model. Using the backfitting results, we conclude that the Tree and CART model algorithm using densities performs most accurately. That is in agreement with findings by Huettmann and Diamond (2001). Ideally, we would evaluate our predictive models using methods detailed in Fielding and Bell (1997), Pearce and Ferrier (2000), and Manel et al. (2001). However, we require additional and alternative density survey data, which presently does not exist for British Columbia. Although the model results varied, Fig. 5 show that the overall trends for the predictions are very similar and lie within a relatively small range for all non-linear algorithms. This suggests that the actual modelling algorithms do not affect the findings and conclusions overall. Likely, the research/survey design and data quality is great importance and should be designed with care.

Our estimated population sizes for Marbled Murrelets in BC waters, within 1 km to shore are between 165,000 and 185,000 individuals. These numbers are much higher than those presented by Rodway et al. (1992) and Burger (personal communication) but are not really comparable. These numbers likely present the maximum carrying capacities for BC marine waters. But since these numbers refer to the period when density surveys where carried out (1972–1993), recent estimates of approximately 60,000 birds could still suggest a decline, likely due to habitat loss (Ralph et al., 1995; Nelson, 1997). Our models are based on the marine environment alone and thus likely show where these birds can be found at the coast on a 10-km scale. Real numbers could be lower, due to other variables such as predators and other distribution limiting factors. More investigations are needed to further clarify this topic.

Increasing proximity to old-growth forest increases the predicted Tree-SPLUS density and GLM standard error (Fig. 7). Most of the predicted values, close to old-growth forests (<5 km to old-growth patch) had high Murrelet numbers as well as high standard errors. Birds found in regions A and B (Fig. 7) have a higher chance of being breeders, since they are found closer to old-growth forests. However, since breeders are normally found solitarily or in pairs, it is less likely for breeders to be found in region B, where birds are in high densities, than in region A, where birds are more dispersed. Birds within region C are likely to be non-breeders ('floaters') due to commuting constraints during the nesting period. We presume the proximity to old-growth forests can affect both the numbers of Marbled Murrelets observed and their fluctuations. We hypothesize that breeders are found closer to the old-growth forest (A), while non-breeders can be found either very close (B) or very far from old-growth forest (C).

In summary, this study has demonstrated Murrelet response to their marine environment through a modelling application. We evaluated multiple algorithm predictions on the little known distribution of a threatened species and studied on a scale that is relevant for its management in British Columbia. Developing a marine model, and explaining outliers (residuals) using terrestrial features, draws a link between both ecosystems that were previously seen as independent from each other. We suggest similar approaches be of major importance for species like Marbled Murrelets, which depend on both marine and terrestrial habitats. Further, we suggest applying similar approaches and methods to Marbled Murrelets and seabirds of the en-

tire Pacific. The establishment of centralized and high quality databases for Marbled Murrelets and their marine and terrestrial habitats are crucial concepts to assure effective conservation for this species of international concern.

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