HABITAT SELECTION BY KITTLITZ'S *BRACHYRAMPHUS BREVIROSTRIS* AND MARBLED MURRELETS *B. MARMORATUS* IN HARRIMAN FJORD, PRINCE WILLIAM SOUND, ALASKA

SHAWN W. STEPHENSEN[1], DAVID B. IRONS[2], WILLIAM D. OSTRAND[3] & KATHERINE J. KULETZ[2]

[1]*Oregon Coast National Wildlife Refuge Complex, 2127 SE Marine Science Drive, Newport, Oregon 97365, USA (shawn_stephensen@fws.gov)*
[2]*US Fish and Wildlife Service, Migratory Bird Management, 1011 East Tudor Road, Anchorage, Alaska 99503, USA*
[3]*13540 Westwind Dr., Anchorage, Alaska 99516, USA*

Received 2 September 2015, accepted 24 December 2015

SUMMARY

STEPHENSEN, S.W., IRONS, D.B., OSTRAND, W.D. & KULETZ, K.J. 2015. Habitat selection by Kittlitz's *Brachyramphus brevirostris* and Marbled murrelets *B. marmoratus* in Harriman Fjord, Prince William Sound, Alaska. *Marine Ornithology* 44: 31–42.

Kittlitz's Murrelet *Brachyramphus brevirostris* is a rare seabird found in glacial waters of coastal Alaska and Siberia. Survey data have indicated population declines since the 1980s and, as a result, in 2004 the species became a candidate for listing under the *Endangered Species Act*. Factors that may have contributed to the population decline include human disturbance and glacial retreat. In our study, conducted in Harriman Fjord of Prince William Sound (PWS), Alaska, we defined the characteristics of the marine habitat, including water column characteristics, selected by Kittlitz's and Marbled murrelets *B. marmoratus* through the two phases of the breeding cycle: incubation and chick-rearing. We also examined habitat selection for both species with respect to geographic variables (distance to glacier, distance to sill and distance to shore) and water column characteristics (conductivity, temperature, turbidity and depth). Our results indicate that Marbled Murrelets are associated with deep, clear water far removed from glaciers. In contrast, Kittlitz's Murrelets are associated with turbid, cold, shallow, fresh water close to glaciers and glacial moraine sills. These data indicate that the two species occupy different areas within the fjord, although with some overlap, related to geographic variables and water column characteristics specific to each species.

Key words: Kittlitz's Murrelet, *Brachyramphus brevirostris*, Marbled Murrelet, *Brachyramphus marmoratus*, Prince William Sound, habitat models, water column parameters, geographic variables

INTRODUCTION

The Kittlitz's Murrelet *Brachyramphus brevirostris*, a boreal–low Arctic species, is one of the rarest seabirds in North America and is found in isolated populations at specific sites in coastal Alaska and Siberia. The Alaska population represents approximately 95% of the world population (Day *et al*. 1999). Surveys by the US Fish and Wildlife Service (USFWS) and US Geological Survey (USGS) have indicated large declines in regional populations between the 1980s and 2000, including in Prince William Sound (PWS; Kuletz *et al*. 2011a), Lower Cook Inlet (Kuletz *et al.* 2011b) and Glacier Bay, Alaska (Piatt *et al.* 2011). Because of concerns for the status of Kittlitz's Murrelet, it became a candidate for the Endangered Species List (USFWS 2004), but it was not listed due to uncertainty about further declines and inability to identify specific threats (USFWS 2013). Today, the PWS population of Kittlitz's Murrelet is estimated to comprise 4% of the world population (USFWS 2013), and the species remains a species of concern according to conservation groups such as the International Union for Conservation of Nature and BirdLife International.

The Marbled Murrelet *B. marmoratus* is a northeastern Pacific temperate–boreal species (Gaston & Jones 1998, Nelson 1997). The species' populations have declined in some locations in British Columbia and Alaska (Piatt *et al*. 2007), and it was listed as threatened in Canada in 1990 and in the southern portion of its range in the United States in 1992 (USFWS 1992). Populations in the northern Gulf of Alaska appear to have declined by 50%–73% over the last 17–20 years (Piatt *et al*. 2007).

Kittlitz's and Marbled murrelets are closely related and may exhibit extensive niche overlap, including prey preferences, foraging habitat and diving behavior (Day & Nigro 1998, Day *et al.* 2003, Arimitsu *et al*. 2011). However, some niche separation exists: Kittlitz's Murrelets are more closely associated with glacial areas (Day & Nigro 2000, Day *et al*. 2003) and eat a higher proportion of invertebrates than Marbled Murrelets (Day *et al*. 1999).

The overall goal of this study was to more specifically define the differences between Kittlitz's and Marbled murrelets in their use of marine habitats, and to describe the marine habitat characteristics selected by these species in glacially affected Harriman Fjord of PWS. We selected Harriman Fjord because Kuletz *et al*. (2003) found that 85% of the estimated PWS Kittlitz's population in 2001 was located in the northwest corner of PWS, including Harriman Fjord, and the area also supported high densities of Marbled Murrelets. We tested the hypotheses that Kittlitz's Murrelets are associated with more turbid glacial water in comparison with Marbled Murrelets, and that Kittlitz's and Marbled murrelets select different habitats. We determined the distribution and abundance (densities) of both murrelet species, measured water column characteristics and geographic variables, and examined the relationship between bird density and these variables.

STUDY AREA

Prince William Sound, Alaska, is an estuarine embayment of 10000 km^2 located in the northern Gulf of Alaska (Fig. 1) and bordered by the Chugach Mountain range on the north and east and the Kenai Mountains on the west. Terrestrial vegetation consists of conifers, shrubs and forbs, and is distributed at different elevations within PWS. The coastline (more than 5000 km) is rugged, with numerous tidewater glaciers, deep fjords and islands. The region has cool temperatures, heavy cloud cover, high humidity, frequent strong winds and a mean annual precipitation of 1.6 m (Wilson & Overland 1986). Water circulation is dominated by the Alaska Coastal Current (ACC), which periodically enters PWS through Hinchenbrook Entrance and mixes with a high volume of fresh water input from precipitation, rivers and glaciers (Niebauer *et al.* 1994).

Harriman Fjord (61°03.620′N, 148°17.310′W) is located in northwestern PWS (Fig. 1) and is connected to the main body of PWS via Barry Arm in Port Wells. The fjord occupies an area of 65.6 km^2 with five tidewater and numerous hanging glaciers (Molnia 2001). During summer months, glaciers calve constantly, leaving portions of the fjord ice-choked with various sizes of brash ice. Glacial-fed streams from both tidewater and hanging glaciers contribute a high volume of fresh water (Wang *et al*. 2001, Weingartner *et al*. 2005). The glacial fjord is generally deep (150 m), although shallow glacial moraine sills (5–50 m) are located at the mouths of Barry Arm and Surprise Inlet (Fig. 1).

METHODS

Murrelet surveys

We conducted boat-based counts of Kittlitz's and Marbled murrelets in 2004 during June (early summer) and July–August (late summer), corresponding, respectively, to incubation and chick-rearing periods. We scheduled the surveys for mid-cycle of each spring and neap tide series because of the possible influence of tidal phase on murrelet foraging (Allyn *et al.* 2012). Counts occurred within a 1 × 1 km grid starting at a randomly selected location; cross-fjord transect lines roughly perpendicular to the shoreline as well as along-shore transect lines were followed to estimate bird abundance (Fig. 2). We surveyed from an 8 m fiberglass boat traveling at ~9.3–14.8 km/h (5–8 knots). We skipped every other transect to minimize recounting birds that might flush from the surveyed transect; we then surveyed the skipped transect 1 h later. The boat maintained a 200 m distance from tidewater glaciers while on transect.

We used standard survey protocols for small vessels (Gould & Forsell 1989), using two observers and one boat driver who assisted in sightings. Observers used 10× binoculars for species

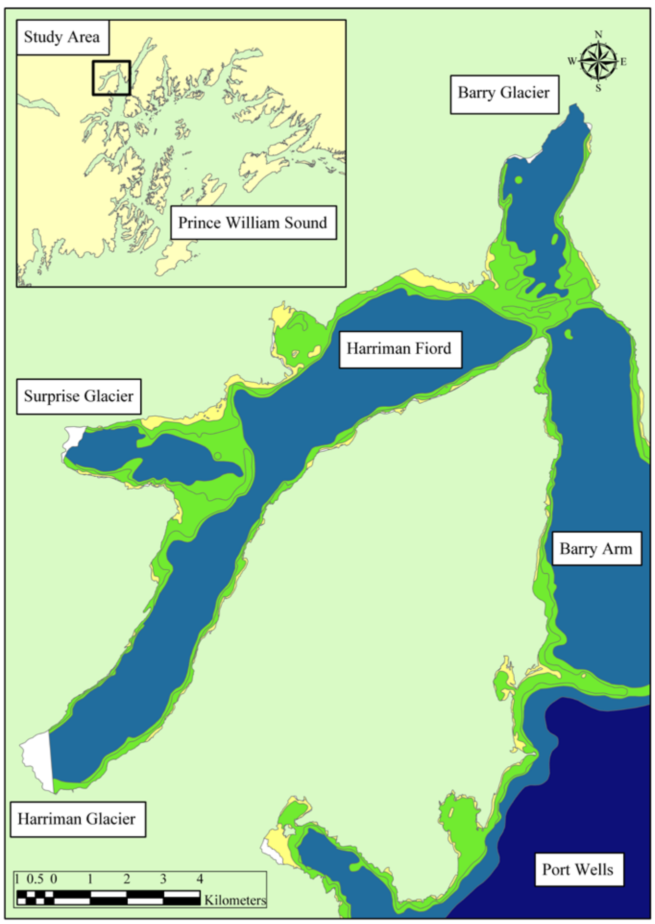


Fig. 1. Harriman Fjord, Prince William Sound, Alaska, study area. Bathymetry intervals are indicated by colored shading (yellow: 1–1.8 m [0–1 fathom], green: 1.8–18.3 m [1–10 fathoms], blue: >18.3 m [>10 fathoms]).

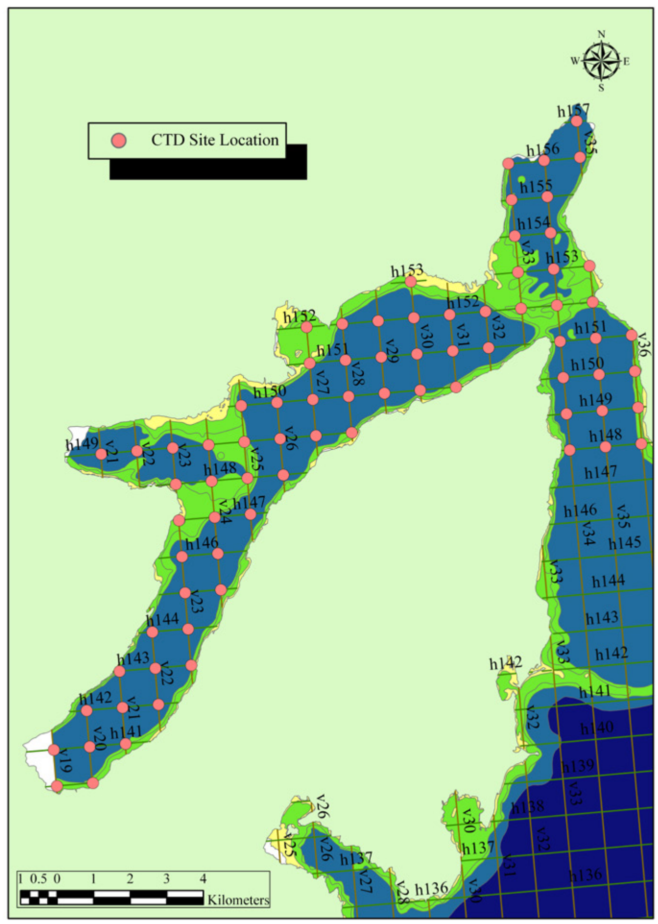


Fig. 2. Harriman Fjord with pelagic transects and CTD sample site locations. CTD sample sites are at the horizontal and vertical line intersections. Bathymetry intervals are indicated by colored shading (yellow: 1–1.8 m [0–1 fathom], green: 1.8–18.3 m [1–10 fathoms], blue: >18.3 m [>10 fathoms]).

identification and recorded species, number, group type (single, pair, or group) and distance (perpendicular to boat) in 25 m intervals for every murrelet on the water and in the air within 100 m of each side and 100 m ahead of the boat. Birds ≤200 m offshore were recorded as shoreline and those >200 m were recorded as pelagic. All observations were entered directly into DLOG (R.G. Ford, Inc., Portland, OR), a computer program with a global positioning system (GPS) interface that assigns a latitude and longitude to each entry as well as tracks location, environmental and observer conditions at 20 s intervals. We conducted surveys between 06h00 and 17h30 (Alaska Daylight Savings Time). We restricted acceptable survey conditions to seas <1.3 m and visibility >100 m.

Water column characteristics

Previous studies indicated that murrelets forage in shallow water (<60 m) and use the upper portion of the water column (Day & Nigro 1998, Hamilton *et al*. 2005). Therefore we examined both surface and water column characteristics to 30 m depth. We measured water surface and water column variables with an SBE-19 Seacat CTD Profiler (Sea-Bird Electronics, Bellevue, WA), as well as with a Secchi disk. "CTD" is an abbreviated name for an instrument package that includes sensors for measuring conductivity, temperature, and depth of seawater. Water column variables included electrical conductivity (Siemens/meter; [S/m]) as a measure of salinity, temperature (Celsius; °C), pressure (depth, m) and turbidity (nephelometric turbidity unit, NTU). A suspended solids and turbidity monitor was attached to the CTD profiler. The monitor used an optical sensor for measuring turbidity and suspended solids concentrations by detecting infrared radiation scattered from suspended matter. The CTD profiler was attached to a line marked at 10 m increments. We set the sampling rate at 0.5 s and lowered and raised the CTD profiler at approximately 0.7 m/s with an electric winch. CTD samples were taken at the intersections of the grid lines (Fig. 2). The CTD profiler was lowered through the water column until it reached approximately 10 m from the ocean floor (determined by a depth sounder). We used only the descent data for analysis because the CTD profiler could change or alter the water column characteristics as it traveled through the water. We retrieved the data from the CTD profiler and downloaded them to a laptop computer with SeaTerm version 1.48, Sea-Bird Electronics. The raw CTD data were processed with Sea-Bird Electronics Data Processing software (version 5.13a Sea-Bird Electronics, Inc. 2004). The data were converted, filtered, aligned, derived and binned during the process procedure. In addition, water surface turbidity was measured at each CTD site with a Secchi disk to the nearest 0.1 m.

The CTD data were divided into 1 m (water surface) and 30 m (water column) categories. We calculated the means of the 1 m surface, and means and variance of water column variables such as temperature, turbidity, conductivity and Secchi depth. The physical characteristics of the water column measured with the CTD profiler were displayed with Ocean Data View software.

We measured several variables that described the geographic and habitat features at each CTD site as well. These included water depth, distance to glacier, distance to shore and distance to glacial moraine sill. Water depth at each CTD site was measured with the boat sonar. Distance to nearest tidewater glacier (km), distance to shore (km) and distance to glacial moraine sill (km) from each CTD site was measured with ArcMap version 9.2 measure tool.

Data analysis

We tested the hypotheses that Kittlitz's and Marbled murrelets selected different habitats within Harriman Fjord and that these preferences changed during the early versus late summer.

We divided transects into segments of 1 000 m, which included 500 m on either side of each CTD sample site (Fig. 2), and calculated bird densities (birds/km^2) for each segment. We blocked murrelet distributions into 1 km segments for analysis of bird densities versus water column characteristics and habitat features. The density of Kittlitz's and Marbled murrelets for each segment was calculated by multiplying the area surveyed (transect length by width) by the number of observed individuals. The transect segments and total transect lengths were measured with ArcMap version 9.2 measure tool.

We tested all water column variables for normality using the descriptive statistics analysis function of Microsoft Office Excel 2003. Data were considered normally distributed if univariate skewness was ≤2.0 and kurtosis was ≤7.0 (Curran *et al*. 1996). We tested for normality of bird densities by visual inspection of histograms. Those variables that were not normally distributed were normalized by log10 transformations.

Because murrelet density at sea is strongly influenced by breeding phase (Kuletz & Kendall 1998, Kissling *et al.* 2007), we grouped the data and analyzed population distributions separately for the incubation period (17 June to 7 July) and chick-rearing period (9–25 July; Day 1996). A correlation matrix of paired comparisons of all possible combinations of candidate variables for each period was developed using SAS. Variable pairs that had $r \geq 0.5$ were considered correlated and not simultaneously included in models.
We developed three sets of models to describe bird habitat selection: mean (0–30 m), variance (0–30 m) and surface (0–1 m) model sets composed of all possible combinations of candidate variables for each bird species. Eighty-four individual models were used in the variance and mean model sets, and 72 individual models for the surface model set. Each model described the relationship between bird density and the candidate variables. For the final analysis, the models were grouped as Surface and All (0–30 m mean, 0–30 m variance and surface combined) for early summer, late summer and both periods combined.

The relationship between bird density and water column data variables was determined by multi-way analysis of variance (MANOVA) with repeated measures that used individual transects as sample units. We fit MANOVA with repeated measures to all equations within each model set (SAS 2007). The models were ranked based on Akaike's Information Criterion (AIC) corrected for small sample sizes (AICc; Akaike 1973, Burnham & Anderson 2002, Burnham *et al*. 2011). The models with minimum AICc values were selected as the best models (Burnham & Anderson 2002, Burnham *et al.* 2011). AICc differences were calculated between the models, and we used only those models with a difference of ≤1.0 as the best approximating models in the candidate set, as suggested by Burnham and Anderson (2002).

We parameterized a repeated measures regression for bird density by running models with the maximum likelihood (ML) method (set on proc mixed in SAS). The top-ranked models were then run with the proc mixed with restricted maximum likelihood (REML) method to the determined relationship (positive or negative). Model probability and evidence ratio of each best approximating model were calculated (SAS 2013) to measure strength of evidence (Burnham *et al.* 2011). We estimated which were the best models using the AICc scores; the evidence for each model in the set was quantified using model probabilities and evidence ratios.

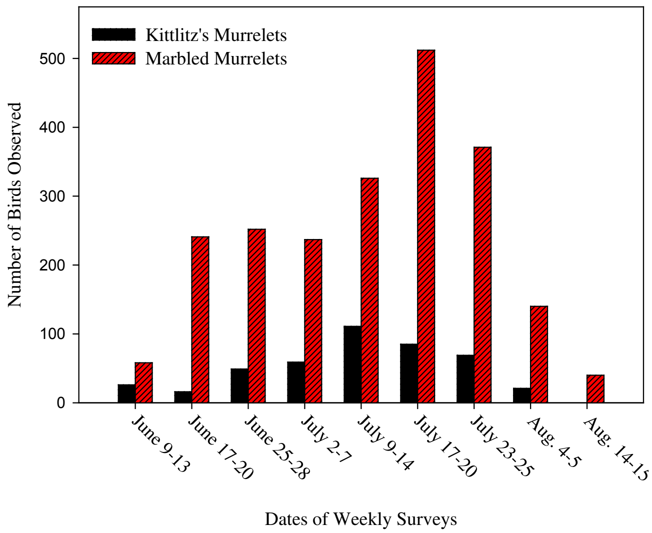


Fig. 3. Total number of Kittlitz's and Marbled Murrelets by week in Harriman Fjord in 2004.

RESULTS

Murrelet abundance and distribution

In Harriman Fjord, Kittlitz's and Marbled murrelet abundance varied throughout the summer (9 June–15 August). Murrelet abundance was low in early summer, peaked midway and tapered off at the end of our study period (Fig. 3). Kittlitz's Murrelet peak abundance (111 individuals) occurred 9–14 July, and Marbled Murrelet peak abundance (514 individuals) occurred 17–20 July. Marbled Murrelets were present through the summer, but we did not observe any Kittlitz's Murrelets during the last week of surveys (Fig. 3). Overall, we observed fewer birds during June and August compared with July (Fig. 3).

The respective distributions of Kittlitz's and Marbled murrelets remained consistent throughout the summer. Kittlitz's Murrelets were concentrated near the glaciers, in shallow water and near glacial moraine sill areas during June and July. Although both species occupied Harriman Arm and the glacial moraine sill areas, Kittlitz's Murrelets were observed in greater densities at the sill areas compared with Marbled Murrelets (Fig. 4). In contrast,

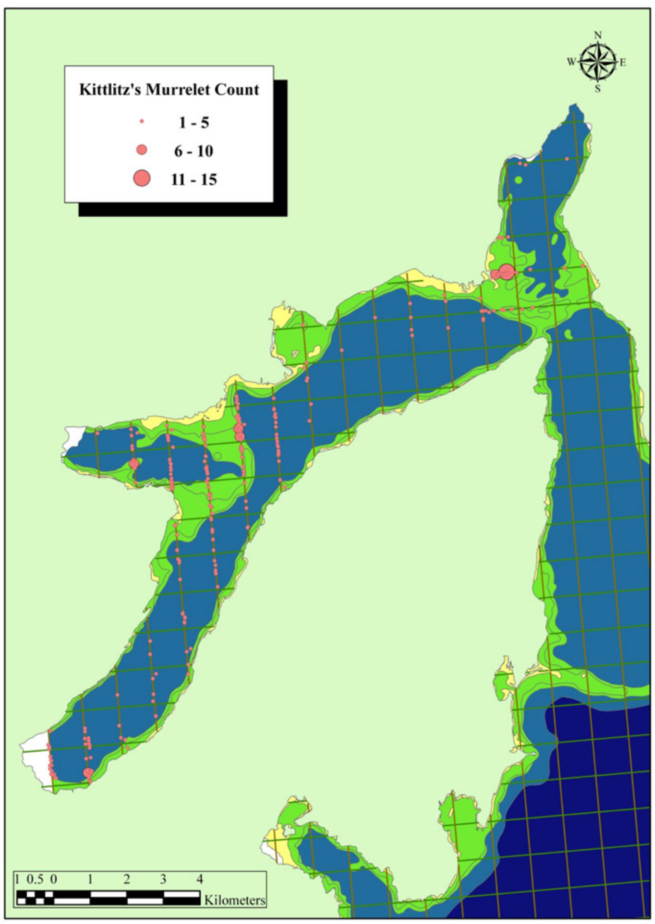


Fig. 4. Kittlitz's Murrelet distribution and abundance in Harriman Fjord during summer (9 June–15 August) 2004. Bathymetry intervals are indicated by colored shading (yellow: 1–1.8 m [0–1 fathom], green: 1.8–18.3 m [1–10 fathoms], blue: >18.3 m [>10 fathoms]).

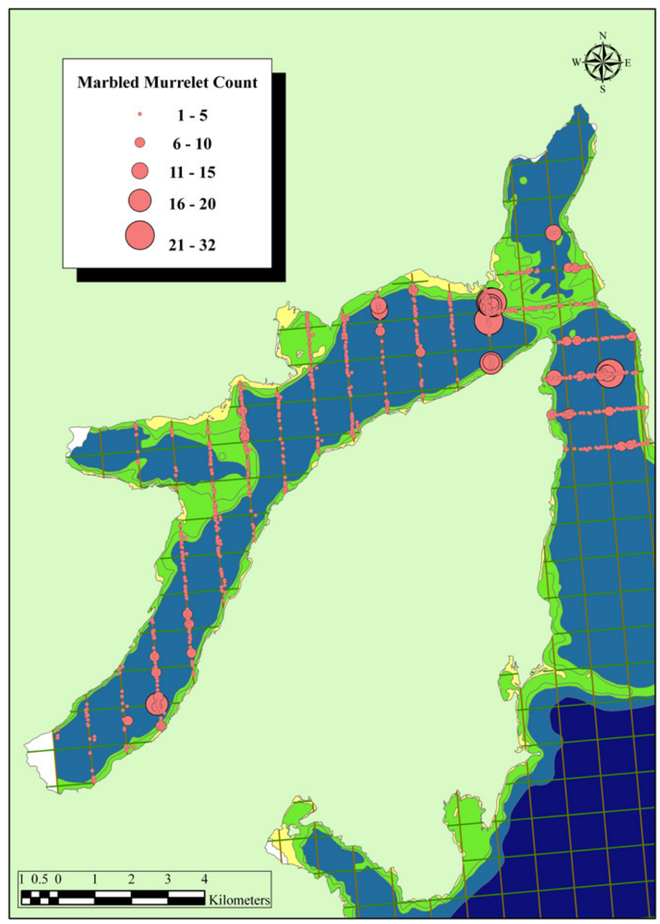
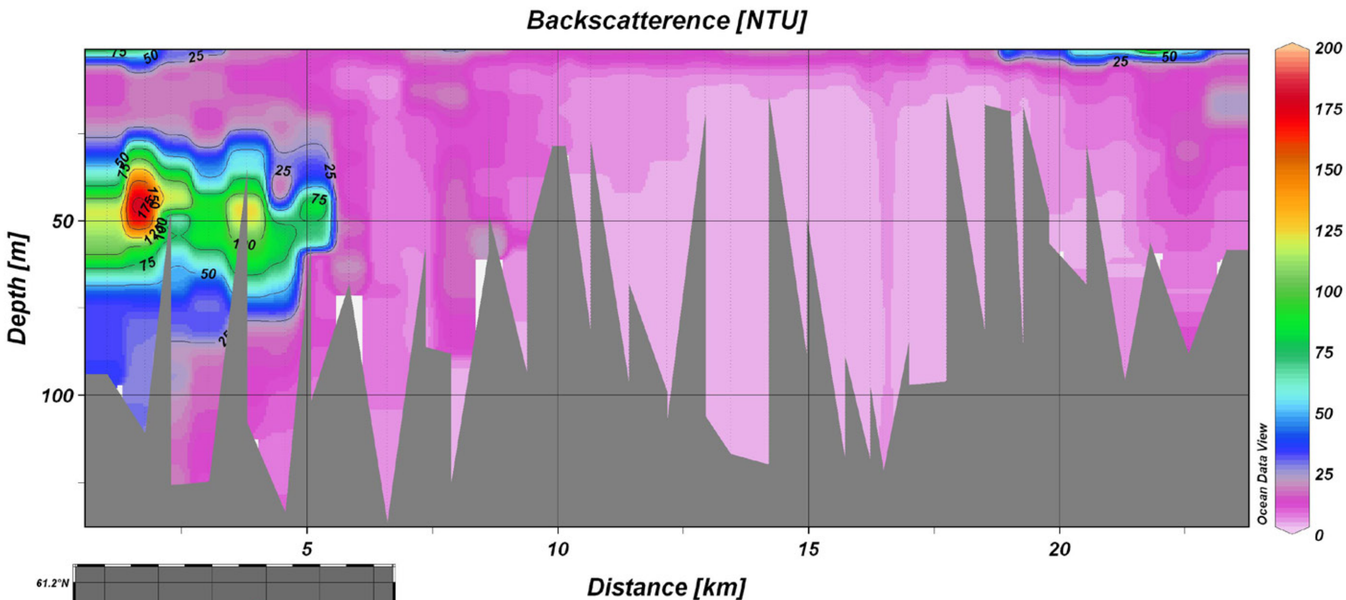


Fig. 5. Marbled Murrelet distribution and abundance in Harriman Fjord during summer (9 June–15 August) 2004. Bathymetry intervals are indicated by colored shading (yellow: 1–1.8 m [0–1 fathom], green: 1.8–18.3 m [1–10 fathoms], blue: >18.3 m [>10 fathoms]).

Marbled Murrelets were distributed more evenly throughout the fjord during June and July, although there were areas of consistently high bird density. However, Marbled Murrelet densities were higher in areas of deep water and farther from glaciers based on raw distributions (with the exception of the west side of the sill between Barry Arm and Harriman Fjord). The Barry Arm area was occupied exclusively by Marbled Murrelets throughout the summer. Other areas with high murrelet density were in upper Barry Arm ~1–2 km south of a shallow sill (Fig. 5).

Water column characteristics

Silty glacial runoff dispersed throughout the water column was most apparent near the tidewater glaciers (Fig. 6). Multiple layers of clear and turbid water were pronounced near the glaciers, and clear uniform water was more prevalent as distance from glaciers increased. Mean turbidity of the surface and water column fluctuated only slightly and remained relatively similar throughout the summer (Table 1).



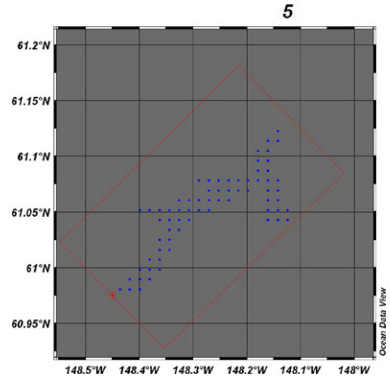


Fig. 6. Water column profile of backscatterence (turbidity) of Harriman Fjord 23–25 July 2004.

TABLE 1
Water surface and column parameter means by week in Harriman Fjord during 2004

Variable[a]	Week 2	Week 3	Week 4	Incubation	Week 5	Week 6	Week 7	Chick-Rearing
Back	1.264	1.179	1.140	1.194	1.262	1.291	1.343	1.300
Cond	2.205	2.372	2.478	2.351	2.073	2.167	1.753	1.994
Temp	6.750	7.927	6.874	7.184	6.866	7.159	6.336	6.783
MBack	0.918	0.796	0.877	0.864	0.974	0.950	1.000	0.975
MCond	2.874	2.896	2.910	2.893	2.855	2.865	2.727	2.814
MTemp	6.010	6.239	6.033	6.094	5.959	6.255	6.507	6.254
VBack	1.241	0.902	0.767	0.970	0.982	1.086	1.315	1.134
VCond	-1.492	-1.747	-1.809	-1.683	-1.369	-1.434	-0.989	-1.259
VTemp	0.137	0.212	0.091	0.147	0.087	0.182	0.208	0.163

[a] Back = backscatterence of water surface (indicative of turbidity), Cond = conductivity of water surface, Temp = temperature of water surface, MBack = mean backscatterence of 30 m water column, MCond = mean conductivity of 30 m water column, MTemp = mean temperature of 30 m water column, VBack = variance backscatterence of 30 m water column, VCond = variance conductivity of 30 m water column, VTemp = variance temperature of 30 m water column.

Conductivity by depth remained constant and varied little throughout the summer in the stratified water column. Conductivity was lower at the surface (Fig. 7, Table 1).

The temperature profile was highly correlated (correlation matrix) to the turbidity profile. Cold turbid water layers were found at various depths near the glaciers. The surface temperature (upper 5 m) was slightly higher than the remainder of the column (Fig. 8).

Murrelet distribution relative to water column characteristics

Kittlitz's Murrelet densities were negatively correlated with Secchi depth, mean water temperature, water depth, conductivity, mean conductivity, distance to glacier and distance to glacial moraine sill (Tables 2–4). Marbled Murrelet densities were positively correlated with water depth and distance to glacier and negatively correlated with surface backscatterence and mean backscatterence (Tables 2–4).

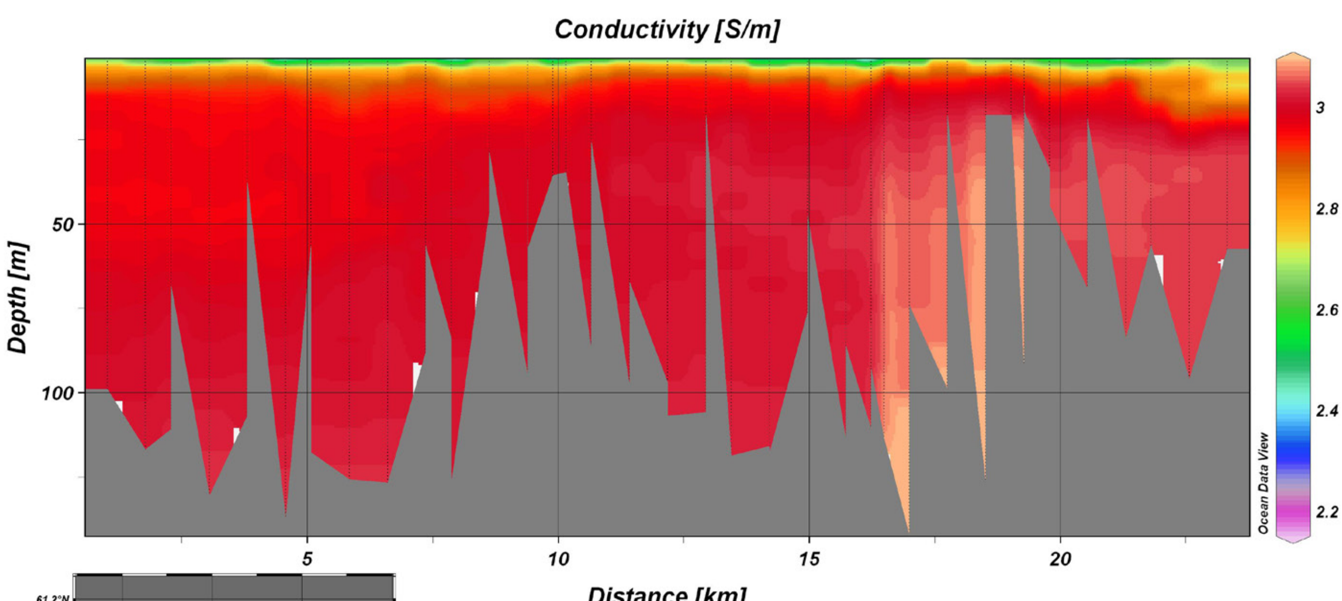
Early summer

The models with the lowest AICc score, model probability of 0.500 and evidence ratio of 1.000 were selected as the best models to describe murrelet densities during the early and late summer periods.

Surface models: The surface models included only surface candidate variables to describe murrelet distribution and densities. The surface model that best described Marbled Murrelet densities included water depth, distance to glacier and distance to sill (Table 2). Marbled Murrelet densities were positively correlated with water depth and distance to glacier, and negatively correlated with distance to sill (Table 2). In summary, Marbled Murrelets preferred deep water far from the glaciers and close to the sill during early summer.

For Kittlitz's Murrelets, the surface model that best described densities included Secchi depth, water depth and distance to shore. Five other models had a ΔAICc of ≤1.0 with different combinations of Secchi depth, water depth, distance to shore, conductivity, distance to glacier and distance to sill. The Kittlitz's Murrelet density was negatively correlated with all model variables except distance to shore. The top-ranked model fit these data 1.29 to 1.52 times better than the other models according to the evidence ratio (Table 2). Thus, Kittlitz's Murrelets were found far from shore in shallow water with high surface turbidity during early summer (Table 2).

All models: When all models (0–30 m mean, 0–30 m variance and surface) were combined, density of Marbled Murrelets was best described by a single model that included water depth, mean backscatterence and distance to sill. Marbled Murrelet density was negatively correlated with mean backscatterence and distance to sill, and positively correlated with water depth (Table 2). These data indicated that Marbled Murrelets selected sites with deep and clear water throughout the top 30 m of the water column; however, they were also found close to sills. Kittlitz's Murrelet densities were best described by the model that included Secchi depth, water depth and distance to shore. The top-ranking models were the same for surface and all models grouping during early summer (Table 2).



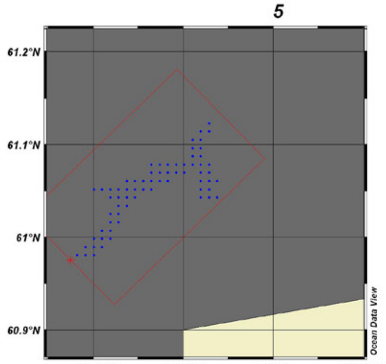


Fig. 7. Water column profile of conductivity (salinity) of Harriman Fjord 2–7 July 2004.

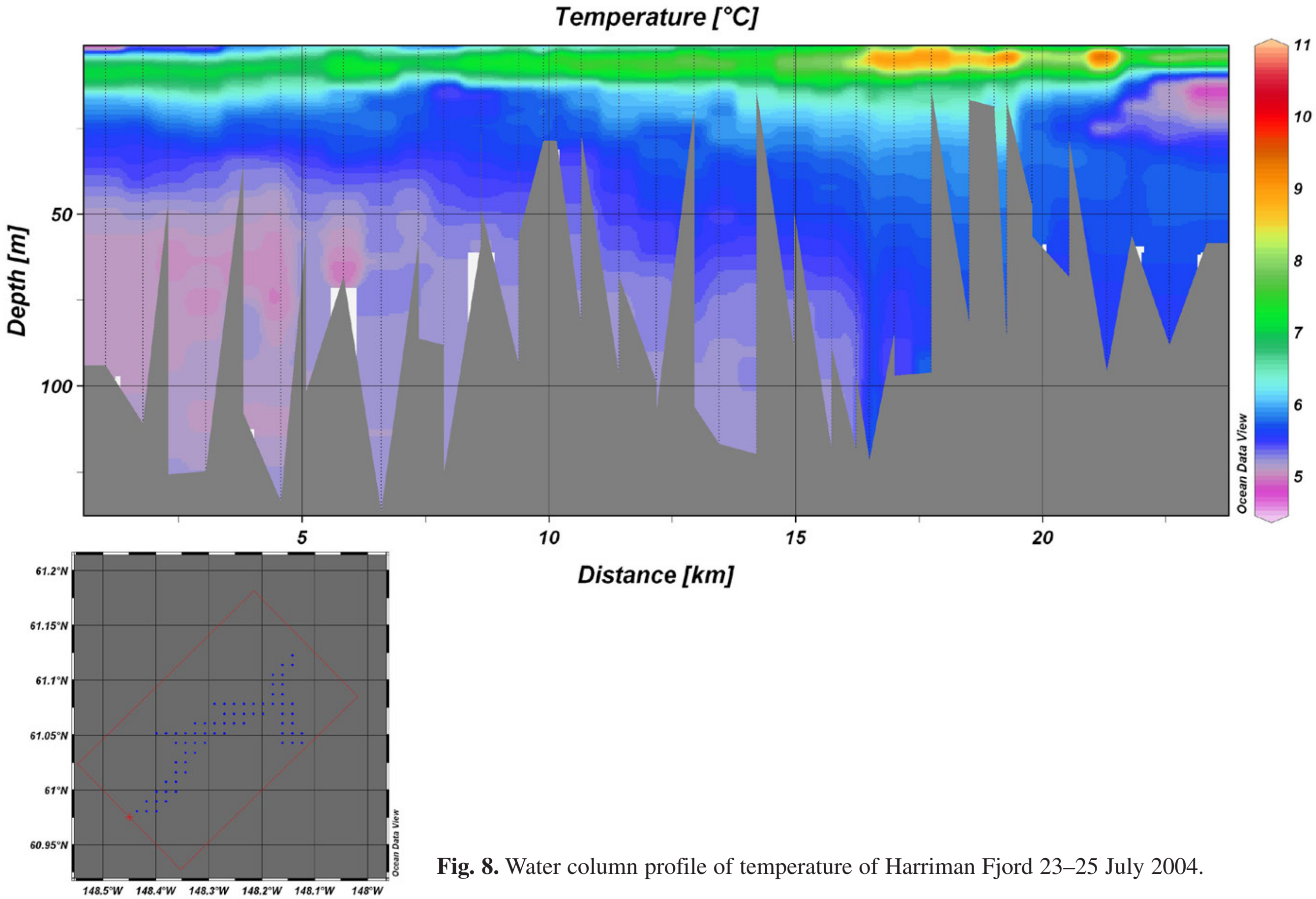


Fig. 8. Water column profile of temperature of Harriman Fjord 23–25 July 2004.

TABLE 2
Models of the relationships among murrelets and variables early summer (murrelet incubation period) for Harriman Fjord, Alaska

Species	AICc	ΔAICc	Models	Model probability	Evidence ratio	(Relationship) model variables[a]
MAMU	421.9	0.0	Surface	0.500	1.000	(+) Depth, (+) Distance to Glacier, (-) Distance to Sill
KIMU	231.1	0.0	Surface	0.500	1.000	(-) Secchi, (-) Depth, (+) Distance to Shore
KIMU	231.5	0.4	Surface	0.437	1.290	(-) Secchi, (-) Depth
KIMU	231.5	0.4	Surface	0.413	1.423	(-) Secchi
KIMU	231.7	0.6	Surface	0.439	1.280	(-) Conductivity, (-) Depth, (-) Distance to Glacier, (+) Distance to Shore
KIMU	231.8	0.7	Surface	0.412	1.428	(-) Depth, (-) Distance to Glacier, (+) Distance to Shore
KIMU	231.8	0.7	Surface	0.397	1.522	(-) Secchi, (-) Distance to Sill
MAMU	418.7	0.0	All models	0.500	1.000	(+) Depth, (-) Mean Backscatterence, (-) Distance to Sill
KIMU	231.1	0.0	All models	0.500	1.000	(-) Secchi, (-) Depth, (+) Distance to Shore
KIMU	231.5	0.4	All models	0.452	1.212	(-) Secchi, (-) Depth
KIMU	231.5	0.4	All models	0.441	1.269	(-) Secchi
KIMU	231.7	0.6	All models	0.420	1.379	(-) Conductivity, (-) Depth, (-) Distance to Glacier, (+) Distance to Shore
KIMU	231.8	0.7	All models	0.412	1.428	(-) Depth, (-) Distance to Glacier, (+) Distance to Shore
KIMU	231.8	0.7	All models	0.412	1.430	(-) Secchi, (-) Distance to Sill

MAMU = Marbled Murrelet, KIMU = Kittlitz's Murrelet.
[a] Positive (+) or negative (-) relationship between model variables and dependent variables ().

Late summer

Surface models: Marbled Murrelet densities were best explained by a single surface model during late summer. The best model included the variables backscatterence, distance to glacier, distance to shore and distance to sill. The model variables backscatterence and distance to sill had a negative relationship, and distance to glacier and distance to shore a positive relationship. Therefore, Marbled Murrelets were observed at sites with clear surface water close to the sill and far from the glaciers and shore (Table 3). The top-ranked model for Kittlitz's Murrelets included conductivity, distance to glacier and distance to sill. Three other models had ≤1.0 ΔAICc and included conductivity, water depth, distance to glacier and distance to sill as model variables in different combinations. All variables within the models were negatively related to Kittlitz's Murrelet densities. Therefore, Kittlitz's Murrelets were observed in shallow, fresh surface water close to the glacial moraine sills and glaciers during the late summer (Table 3). The top-ranked model fit these data 1.28 to 1.56 times better than the other three models, according to the evidence ratio.

All models: The same single model that explained Marbled Murrelet densities in the surface model set was also the single top-ranked model in the all-models set (backscatterence, distance to glacier, distance to shore and distance to sill). Marbled Murrelet densities were negatively correlated with backscatterence and distance to sill and positively correlated with distance to shore and distance to glacier. Even though water column variables (30 m variance and mean) were added to the set of models, we concluded that Marbled Murrelet densities were best explained by surface backscatterence as well as distances to glacier, sill and shore, based on model parameters. Once again, the models indicated Marbled Murrelets

TABLE 3
Models of the relationships among murrelets and variables during chick-rearing period for Harriman Fjord, Alaska

Species	AICc	ΔAICc	Models	Model probability	Evidence ratio	(Relationship) model variables[a]
MAMU	388.7	0.0	Surface	0.500	1.000	(-) Backscatterence, (+) Distance to Glacier, (+) Distance to Shore, (-) Distance to Sill
KIMU	294.4	0.0	Surface	0.500	1.000	(-) Conductivity, (-) Distance to Glacier, (-) Distance to Sill
KIMU	294.9	0.5	Surface	0.438	1.281	(-) Conductivity, (-) Distance to Sill
KIMU	294.9	0.5	Surface	0.437	1.288	(-) Conductivity, (-) Depth, (-) Distance to Sill
KIMU	295.3	0.9	Surface	0.390	1.563	(-) Conductivity, (-) Depth, (-) Distance to Glacier, (-) Distance to Sill
MAMU	388.7	0.0	All Models	0.500	1.000	(-) Backscatterence, (+) Distance to Glacier, (+) Distance to Shore, (-) Distance to Sill
KIMU	292.7	0.0	All Models	0.500	1.000	(-) Mean Temperature, (-) Mean Conductivity, (-) Distance to Sill
KIMU	293.4	0.7	All Models	0.410	1.442	(-) Mean Temperature, (-) Mean Backscatterence, (-) Mean Conductivity, (-) Distance to Sill
KIMU	293.5	0.8	All Models	0.406	1.466	(-) Depth, (-) Mean Temperature, (-) Mean Conductivity, (-) Distance to Sill

MAMU = Marbled Murrelet, KIMU = Kittlitz's Murrelet.
[a] Positive (+) or negative (-) relationship between model variable and dependent variable.

TABLE 4
Models of the relationships among murrelets and variables during incubation and chick-rearing periods for Harriman Fjord, Alaska

Species	AICc	ΔAICc	Models	Model probability	Evidence ratio	(Relationship) model variables[a]
MAMU	818.4	0.0	Surface	0.500	1.000	(-) Backscatterence, (+) Distance to Glacier, (+) Distance to Shore, (-) Distance to Sill
KIMU	537.0	0.0	Surface	0.500	1.000	(-) Conductivity, (-) Depth, (-) Distance to Glacier, (+) Distance to Shore, (-) Distance to Sill
MAMU	818.4	0.0	All models	0.500	1.000	(-) Backscatterence, (+) Distance to Glacier, (+) Distance to Shore, (-) Distance to Sill
KIMU	537.0	0.0	All models	0.500	1.000	(-) Conductivity, (-) Depth, (-) Distance to Glacier, (+) Distance to Shore, (-) Distance to Sill

MAMU = Marbled Murrelet; KIMU = Kittlitz's Murrelet.
[a] Positive (+) or negative (-) relationship between model variable and dependent variable.

preferred clear surface water close to the sill and far from the glacier and shore. Kittlitz's Murrelet densities were best explained by a model that included mean temperature and conductivity, and distance to sill. The second- and third-ranked models included mean temperature, backscatterence and conductivity, as well as distance to sill and water-depth combinations. All model variable relationships were negative; thus, Kittlitz's Murrelets were found in cold, fresh water, throughout the top 30 m of the water column, and close to the glacial moraine sill during late summer (Table 3). The top-ranked model fit these data nearly 1.5 times better than the other two models, according to the evidence ratio.

Entire summer period

Data from the early and late summer periods were combined to obtain a comprehensive view of habitat variables selected by the murrelets during the entire summer period (Table 4).

Surface models: Marbled Murrelet densities were best explained by a single surface model with variables backscatterence, distance to glacier, distance to shore and distance to sill. Marbled Murrelet densities were negatively related to backscatterence and distance to sill and positively correlated with distance to glacier and distance to shore (Table 4). Thus, Marbled Murrelets were found in clear surface water close to the sill and far from the glacier and shore. The model that best explained Kittlitz's Murrelet densities had variables conductivity, water depth, distance to glacier, distance to shore and distance to sill. Thus, Kittlitz's Murrelets selected fresh surface water far from shore in shallow areas close to glaciers and sills during the entire summer period (Table 4).

All models: Both Marbled and Kittlitz's murrelet densities were explained by the same single top-ranked models of the surface and all models sets (Table 4). Marbled Murrelet densities were negatively correlated with backscatterence and positively correlated with distance to glacier, whereas Kittlitz's Murrelet densities were defined by conductivity, water depth, distance to glacier, distance to shore and distance to sill, and were negatively correlated with all variables except distance to shore.

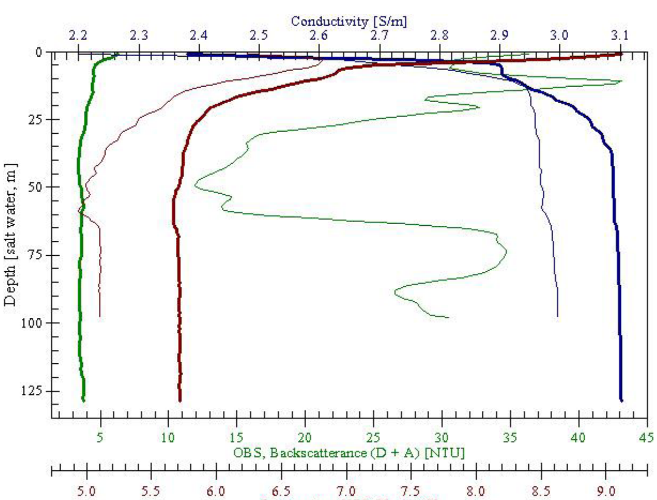


Fig. 9. Kittlitz's and Marbled Murrelets high-density areas and water column profiles (conductivity — blue, backscatterence — green, temperature — red) of Harriman Fjord in 2004. Kittlitz's and Marbled Murrelets hotspot variables indicated with thin lines and thick lines, respectively.

DISCUSSION

Murrelets and water column characteristics

We investigated the relationship between water column characteristics and murrelet distributions, focusing on both surface water (<1 m deep) and water column characteristics to 30 m depth. We limited the analysis to 30 m depth because this is likely the maximum dive depth of murrelets. The diving depths of Marbled and Kittlitz's murrelets have not been measured directly; only dive duration and surface intervals have been documented (Day & Nigro 2000). Equations that calculated dive depth predicted a Marbled Murrelet should be able to reach 47 m (Burger 1991). Hamilton *et al*. (2005) predicted the maximum diving depth of murrelets would be 25 m, and murrelets likely dive to depths of <21 m to capture prey. Most observations of diving murrelets have been made where water depth is <30 m (Burger 1991, Jodice & Collopy 1999). The data indicated that both murrelet species are selecting forage sites based on surface variables, whereas full water column variables were not in the top-ranked models.

Kittlitz's and Marbled murrelets were consistently found at certain locations in Harriman Fjord throughout the summer of 2004. Locations where the murrelets were observed at high densities each week were referred to as "high-density areas." Certain water column characteristics at the high-density areas were relatively consistent, and these characteristics were also those that were included in the top-ranking AICc models. High densities of Kittlitz's Murrelets were observed where the water was shallow, turbid, fresh and cold. In comparison, one of the sites with the highest densities of Marbled Murrelet was located where the water was deep, clear, salty and warm (Fig. 9).

Our results characterizing both the surface and water column were similar to those of Day *et al.* (2003). Marbled Murrelet densities were negatively correlated with turbidity in the surface model with lowest AICc value over the entire breeding season (Table 4). Overall, high densities of Marbled Murrelets were associated with clear surface water. However, Marbled Murrelet densities were negatively related to turbidity during the incubation period (Table 2), which means the birds selected areas in the fjord with clear water throughout the column, not just clear water on the surface.

We found a negative relationship between surface turbidity and Kittlitz's Murrelet density during early summer for surface and all models. In addition, surface turbidity (Secchi depth) was a parameter in most models (Table 2). During the early summer and over the entire summer (incubation and chick-rearing) combined, backscatterence was not a parameter in the top-ranked models for Kittlitz's Murrelets. Therefore, Kittlitz's Murrelets were located in areas with more turbid surface water compared with Marbled Murrelets (Fig. 10). Our study supports others showing that Kittlitz's Murrelets are generally associated with more turbid glacial water in comparison with Marbled Murrelets.

Murrelets and bathymetry

Our study substantiates that *Brachyramphus* murrelets are more abundant >200 m from shore in Harriman Fjord. We had intensive spatial coverage within the fjord and extensive coverage throughout the breeding season (a unique aspect of this study). While both murrelet species were found throughout the fjord, we found more Marbled and Kittlitz's murrelets at distances >200 m from shore. Day & Nigro (2000) indicated that the nearshore zone (≤200 m) is where most individuals are located and where feeding in both species occurs. Radio-tagged Marbled Murrelets were found to use primarily nearshore waters <1 km from shore, although they also used waters farther offshore (Kuletz 2005). Bathymetry may influence murrelet distribution, and we found the highest murrelet densities where waters were <60 m deep in our study area. However, murrelets will feed in deep waters, typically in areas with bathymetric or landscape features that promote upwelling and concentration of prey near the surface (Hunt 1995, Kuletz 2005). Kittlitz's Murrelet densities were negatively correlated with water depth, and this variable was significant in the top-ranked model for the entire summer period (Fig. 11). Bathymetric characteristics can be an important indicator of marine bird-habitat associations because they are fixed in space and can produce hydrological processes such as upwellings, currents and eddies (Yen *et al*. 2005). Upwelling often occurs at glacial moraine sills and at a glacier face and can increase prey abundance and availability (Hunt & Schneider 1987). Both murrelet species were observed at the glacial moraine sill areas, especially Kittlitz's Murrelets during early and late summer (Fig. 12). Kittlitz's Murrelet densities were negatively correlated with distance to sill in the top-ranked model. The aggregation of Kittltiz's Murrelets over glacial fjord sills has been noted in previous studies (Kuletz *et al*. 2003, Allyn *et al*. 2012). Fjord sills may create accessible concentrations of invertebrates and fish that are lifted into the upper water column (Hunt *et al*. 1990, Hunt *et al*. 1999, Coyle *et al*. 1992) and result in high-density areas. In contrast, Day *et al.* (2003) found that Kittlitz's Murrelets avoided marine sills and that marine sills are unimportant to this species for feeding, regardless of the high feeding frequency there. Day *et al.* (2003) also stated that the high feeding frequency but low overall abundance in marine-sill-affected habitats may reflect episodic feeding opportunities such as tidal fronts.

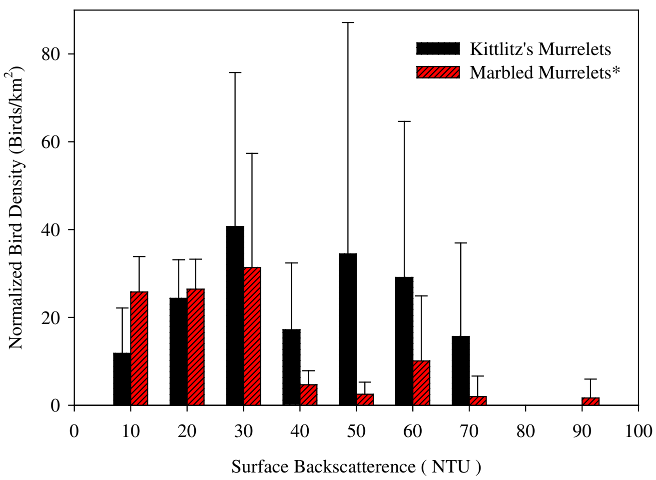


Fig. 10. Normalized densities (birds/km^2) of Marbled and Kittlitz's murrelets in comparison with surface backscatterence (NTU) in Harriman Fjord during summer 2004.

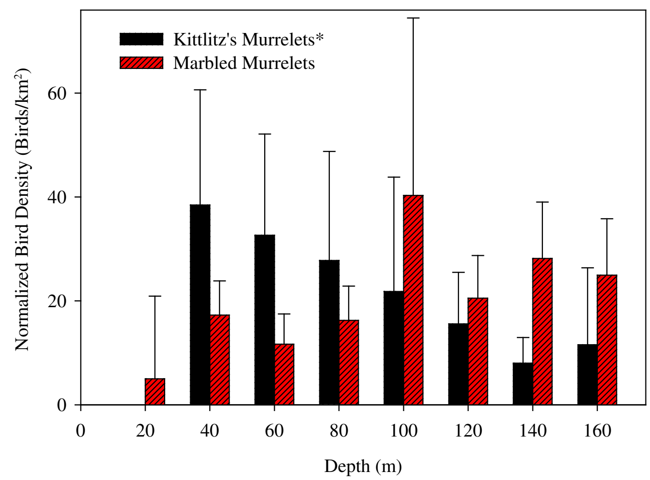


Fig. 11. Normalized densities (birds/km^2) of Marbled and Kittlitz'smMurrelets in comparison with water depth (m) in Harriman Fjord during summer 2004.

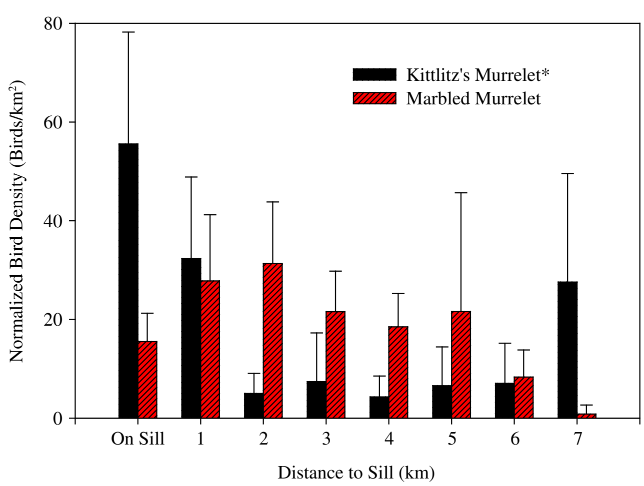


Fig. 12. Normalized densities (birds/km^2) of Marbled and Kittlitz's murrelets in comparison with distance to sill (km) in Harriman Fjord during summer 2004.

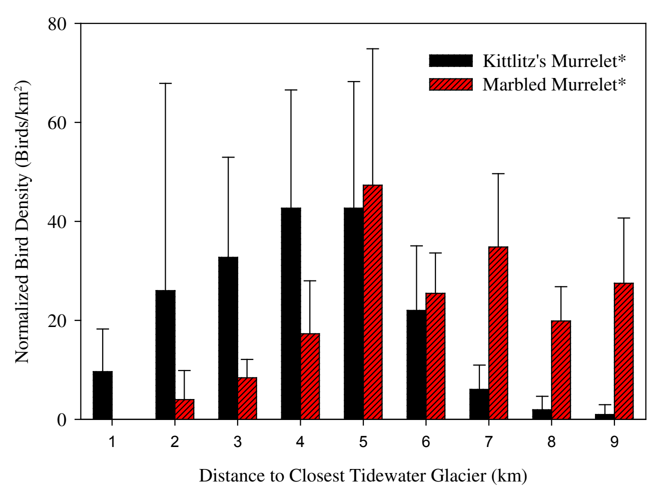


Fig. 13. Normalized densities (birds/km^2) of Marbled and Kittlitz's murrelets in comparison with distance to closest tidewater glacier (km) in Harriman Fjord during summer 2004.

Glacial associations

Distance to nearest tidewater glacier was the strongest and most divergent parameter between the two murrelet species, with Kittlitz's Murrelets more strongly associated with glaciers (Day & Nigro 2000, Day *et al.* 2003, Allyn *et al*. 2015). We found high densities of Kittlitz's Murrelets close to, but Marbled Murrelets at greater distances from the glaciers (Fig. 13). The association with or lack of association with glaciers appears to be the key variable defining niche separation between the two murrelet species.

ACKNOWLEDGEMENTS

Many people and organizations contributed to this project, and with their support came success. Sergei V. Drovetski, Donald E. Spalinger and Douglas Causey provided much-needed support and guidance throughout the project and manuscript writing. Study design assistance was provided by Etienne Danchin (USFWS volunteer), Lymann McDonald (West Inc.) and John F. Piatt (USGS). The US Fish and Wildlife Service, Migratory Bird Management and Ecological Services provided funding and equipment for the project. Volunteers who freely provided countless hours of time and effort included Karen M. Brenneman, Elizabeth A. Labunski, Martin T. Reedy, Kelsey M. Sullivan, Alyson E. McKnight, David R. Sinnett, and Steven Sinnett. Shay Howlin (West Inc.) and Joel Schmutz (USGS) provided statistical and data analysis guidance. Gratitude is expressed to everyone who assisted with and reviewed this manuscript.

REFERENCES

AKAIKE, H. 1973. Information theory as an extension of the maximum likelihood principle. In: PETROV, B.N. & CSAKI, F. (Eds.) *Second International Symposium on Information Theory*. Budapest, Hungary: Akademiai Kaido, pp. 267-281.

ALLYN, A.J., MCKNIGHT, A., MCGARIGAL, K., GRIFFIN, C.R, KULETZ, K.J. & IRONS, D.B. 2012. Relationships among Kittlitz's murrelet habitat use, temperature-depth profiles, and landscape features in Prince William Sound, Alaska, USA. *Marine Ecology Progress Series* 466: 233-247.

ALLYN, A.J., MCKNIGHT, A., MCGARIGAL, K., GRIFFIN, C.R., KULETZ, K.J., CUSHING, D.A. & IRONS, D.B. 2015. Assessing a paired logistic regression model of presence-only data to map important habitat areas of the rare Kittlitz's Murrelet *Brachyramphus brevirostris*. *Marine Ornithology* 43: 65-76.

ARIMITSU, M., PIATT, J.F., ROMANO, M.D. & VAN PELT, T.I. 2011. Status and distribution of the Kittlitz's murrelet *Brachyramphus brevirostris* in Kenai Fjords, Alaska. *Marine Ornithology* 39: 13-22.

BURGER, A.E. 1991. Maximum diving depths and underwater foraging in alcids and penguins. In: MONTEVECCHI, W.A. & GASTON, A.J. (Eds.) *Studies of high-latitude seabirds: 1. Behavioral, energetic, and oceanographic aspects of seabird feeding ecology*. Canadian Wildlife Service Occasional Paper 68. Ottawa, Ontario: Canadian Wildlife Service, pp. 9-15.

BURNHAM, K.P. & ANDERSON, D.R. 2002. *Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach*. 2nd ed. New York, NY: Springer Science+Business Media, Inc.

BURNHAM, K.P., ANDERSON, D.R., & HUYVAERT, K.P. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology* 65: 23-35.

COYLE, K.O., HUNT, J.L. JR, DECKER, M.B. & WEINGARTNER, T.J. 1992. Murre foraging, epibenthic sound scattering and tidal advection over a shoal near St. George Island, Bering Sea. *Marine Ecology Progress Series* 83: 1-14.

CURRAN, P.J., FINCH, J.F. & WEST, S.G. 1996. The robustness of test statistics to nonnormality and specification error in confirmatory factor analysis. *Psychological Methods* 1: 16-29.

DAY, R.H. 1996. Nesting phenology of the Kittlitz's Murrelet. *Condor* 98: 433-437.

DAY, R.H. & NIGRO, D.A. 1998. *Status and ecology of Kittlitz's Murrelet in PrinceWilliam Sound: results of 1996 and 1997 studies*. *Exxon Valdez* Oil Spill Restoration Annual Report, Restoration Project 97142. Anchorage, AK: *Exxon Valdez* Oil Spill Trustee Council.

DAY, R.H. & NIGRO, D.A. 2000. Feeding ecology of Kittltz's Murrelet and Marbled Murrelets in Prince William Sound, Alaska. *Waterbirds* 23: 1-14.

DAY, R.H., KULETZ, K.J. & NIGRO, D.A. 1999. Kittlitz's Murrelet (*Brachyramphus brevirostris*). In: POOLE, A. & GILL, F. (Eds). *The Birds of North America*, No. 435. Washington, D.C. and Philadelphia, PA: The Academy of Natural Sciences and The American Ornithologists' Union.

DAY, R.H., PRICHARD, A.K. & NIGRO, D.A. 2003. Ecological specialization and overlap of *brachyramphus* murrelets in Prince William Sound, Alaska. *Auk* 120: 680-699.

GASTON, A.J. & JONES, I.L. 1998. *Bird Families of the World: the Auks (Alcidae)*. New York: Oxford University Press.

GOULD, P.J. & FORSELL, D.J. 1989. *Techniques for shipboard surveys of marine birds*. Fish and Wildlife Technical Report 25. Washington, D.C.: US Fish and Wildlife Service.

HAMILTON, C.D., GOLIGHTLY, R.T. & TAKEKAWA, J.Y. 2005. Characteristics of diving in radio-marked Xantus's Murrelets. *Marine Ornithology* 33: 155-159.

HUNT, G.L. JR. 1995. Oceanographic processes and marine productivity in waters offshore of marbled murrelet breeding habitat. In: RALPH C.J., HUNT, G.L. JR., RAPHAEL M.G. & PIATT J.F. (Eds.) *Ecology and Conservation of the Marbled Murrelet*. US Department of Agriculture, Forest Service General Technical Report, PSW-GTR-152, pp. 219-222.

HUNT, G.L. JR., HARRISON, N.M. & COONEY, R.T. 1990. The influence of hydrographic structure and prey abundance on foraging of Least Auklets. *Studies in Avian Biology* 14: 7-22.

HUNT, G.L. JR., MEHLUM, F., RUSSELL, R.W., IRONS, D.B., DECKER, M.B. & BECKER, P.H. 1999. Physical processes, prey abundance, and the foraging of seabirds. In: ADAMS, N. & SLOTOW, R. (Eds.) *Proceedings of 22nd International Ornithological Congress*, pp. 2040-2056.

JODICE, R.G.R. & COLLOPY, M.W. 1999. Diving and foraging patterns of Marbled Murrelets (*Brachyramphus marmoratus*): testing predictions from optimal-breathing models. *Canadian Journal of Zoology* 77: 1409-1418.

KISSLING, M.L., REID, M., LUKACS, P.M., GENDE, S.M. & LEWIS, S.B. 2007. Understanding abundance patterns of a declining seabird: implications for monitoring. *Ecological Applications* 17: 2164-2174.

KULETZ, K.J. & KENDALL, S.J. 1998. A productivity index for marbled murrelets in Alaska based on surveys at sea. *Journal of Wildlife Management* 62: 446-460.

KULETZ, K.J., LABUNSKI, E.A. & BRENNEMAN, K.M. 2003. *Distribution and Abundance of Kittlitz's Murrelets in Prince William Sound, Alaska, Summer 2001*. Final Report for Western Alaska Ecological Service. Anchorage, AK: US Fish and Wildlife Service.

KULETZ, K.J. 2005. *Foraging behavior and productivity of a non-colonial seabird, the Marbled Murrelet (Brachyramphus marmoratus), relative to prey and habitat*. PhD dissertation. Victoria, BC: University of Victoria.

KULETZ, K.J., NATIONS, C.S., MANLY, B., ALLYN, A., IRONS, D.B. & McKNIGHT, A. 2011a. Distribution, abundance, and population trends of the Kittlitz's murrelet *Brachyramphus brevirostris* in Prince William Sound, Alaska. *Marine Ornithology* 39: 97-109.

KULETZ, K.J., SPECKMAN, S.G., PIATT, J.F. & LABUNSKI, E.A. 2011b. Distribution, population status and trends of Kittlitz's Murrelet *Brachyramphus brevirostris* in Lower Cook Inlet and Kachemak Bay, Alaska. *Marine Ornithology* 39: 85-95.

MOLNIA, B. 2001. Glaciers of Alaska. *Alaska Geographic* 28 (2).

NELSON, K.S. 1997. Marbled Murrelet (*Brachyramphus marmoratus*). In: POOLE, A. & GILL, F. (Eds). *The Birds of North America*, No. 276. Washington, D.C. and Philadelphia, PA: The Academy of Natural Sciences and The American Ornithologists' Union.

NIBAUER, H.J., ROYER, T.C. & WEINGARTNER, T.J. 1994. Circulation of Prince William Sound, Alaska. *Journal of Geophysical Research* 99: 14.113-14.126.

PIATT, J.F., KULETZ, K.J., BURGER, A.E., HATCH, S.A., FRIESEN, V.L., BIRT, T.P., ARIMITSU, M.L., DREW, G.S., HARDING, A.M.A. & BIXLER, K.S. 2007. *Status review of the Marbled Murrelet (*Brachyramphus marmoratus*) in Alaska and British Columbia.* US Geological Survey Open-File Report 2006–1387, pp. 258.

PIATT, J.F., ARIMITSU, M., DREW, G., MADISON, E.N., BODKIN, J., ROMANO, M.D. 2011. Status and trend of the Kittlitz's murrelet *Brachyramphus brevirostris* in Glacier Bay, Alaska. *Marine Ornithology* 39: 65-75.

US FISH AND WILDLIFE SERVICE (USFWS). 1992. Endangered and threatened wildlife and plants; determination of threatened status for the Washington, Oregon and California population of the Marbled Murrelet. *Federal Register* 57: 45328–45337.

US FISH AND WILDLIFE SERVICE (USFWS). 2004. Endangered and threatened wildlife and plants; review of species that are candidates or proposed for listing as endangered or threatened; annual notice of findings on resubmitted petitions; annual descriptions of progress on listing actions; notice of review; proposed rule. US Department of the Interior, Fish and Wildlife Service. 50 CFR Part 17.69(86), May 4, 2004.

US FISH AND WILDLIFE SERVICE (USFWS). 2013. 12-month finding on a petition to list Kittlitz's murrelet as an endangered or threatened species. *Federal Register* 78: 61764. [Available online at: http://www.fws.gov/alaska/fisheries/endangered/pdf/kittlitzs_murrelet_pr_oct_2013.pdf. Accessed 9 February 2016].

WANG, J., JIN, M., PATRICK, V., ALLEN, J., ESLINGER, D. & COONEY, T. 2001. Numerical simulation of the seasonal ocean circulation patterns and thermohaline structure of Prince William Sound, Alaska using freshwater as a line source. *Fisheries Oceanography* 10(suppl 1): 132-148.

WEINGARTNER, T.J., DANIELSON, S. & ROYER, T.C. 2005. Freshwater variability and predictability in the Alaska Coastal Current. *Deep Sea Res*earch *II* 52: 169-191.

WILSON, J.G. & OVERLAND, J.E. 1986. Meteorology. In: HOOD D.W. & ZIMMERMAN, S.T. (Eds.) *The Gulf of Alaska: Physical Environment and Biological Resources*. US Departments of Commerce and Interior, Minerals Management Service Publication Outer Continental Shelf Study MMS86-0095, pp. 31-54.

YEN, P.P.W., SYDEMAN, W.J., MORGAN, K.H. & WHITNEY, F.A. 2005. Top predator distribution and abundance across the eastern Gulf of Alaska: Temporal variability and ocean habitat associations. *Deep-Sea Research II* 52: 799-822.