ASSESSING A PAIRED LOGISTIC REGRESSION MODEL OF PRESENCE-ONLY DATA TO MAP IMPORTANT HABITAT AREAS OF THE RARE KITTLITZ'S MURRELET *BRACHYRAMPHUS BREVIROSTRIS*

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SUMMARY

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We tested a method for identifying important daytime marine habitat used by the Kittlitz's Murrelet, a rare glacially associated seabird, in Prince William Sound, Alaska. We used a context-dependent modeling framework based on a paired logistic regression model of presence-only data and landscape variables to predict marine habitat used across 17 fjords. Birds used fjords with tidewater glaciers (tidewater glacial fjords) more than fjords without tidewater glaciers (non-tidewater glacial fjords). Within tidewater glacial fjords, birds used shallow waters closer to shore, tidewater glacier faces and glacial moraines more than the average available habitat. Within non-tidewater glacial fjords, birds used habitats that were closer to shore than the average available habitat. Model validation showed the model was robust and performed well; concordance correlation coefficients measuring the agreement between expected and observed proportion of presences were 0.85 and 0.91 for two independent datasets across five probabilities-of-presence bins ranging from 0 to 1. Overall, our approach could assist managers seeking to efficiently delineate important Kittlitz's Murrelet daytime marine habitat areas for conservation in PWS or other regions and for other rare species.

Keywords: *Brachyramphus brevirostris,* Kittlitz's Murrelet, seabird habitat, glaciers, paired logistic regression, case-controlled logistic regression, presence-only data, species distribution model

INTRODUCTION

For rare and threatened species whose populations are difficult to study or monitor we need to develop methods that accurately delineate important habitat areas. Generally, these species lack long-term population data, but conserving important habitat is one of our best short-term strategies for sustaining rare and threatened populations, especially given the pervasive threat of habitat loss and degradation (Wilson 1988, Pimm *et al*. 1995). This conservation approach would be particularly useful for the Kittlitz's Murrelet *Brachyramphus brevirostris*, a rare diving seabird found almost exclusively in Alaskan and Russian waters (Day *et al*. 1999, Artukhin *et al*. 2011). The species' low numbers and population declines in the 1990s and into the early 2000s throughout many core population areas in Alaska (e.g. Arimitsu *et al*. 2011, Piatt *et al*. 2011), including Prince William Sound (PWS) (Kuletz *et al*. 2011), have put this species on numerous conservation lists, including the International Union for Conservation of Nature and Natural Resources Near Threatened List (BirdLife International 2015). These population declines also prompted listing of Kittlitz's Murrelet on the Candidate Endangered Species List (US Fish & Wildlife Service (USFWS) 2011), but it has since been removed owing to stabilized populations and a lack of evidence for direct causes of productivity declines and range-wide population threats (USFWS 2013).

The causes of Kittlitz's Murrelet (hereafter Murrelet) population declines are difficult to determine for several reasons, beginning with the birds' occurrence in remote locations. Further, their cryptic, solitary nesting behavior precludes standard breeding site-based monitoring (Day *et al*. 1999, Kaler *et al*. 2009). Proposed explanations for population declines include spatially explicit anthropogenic factors, such as habitat loss and degradation (Agness *et al*. 2008, USFWS 2011), direct mortality from bycatch (Day *et al*. 1999), and oil spills (van Vliet & McAllister 1994, Kuletz 1996); natural predation may also be an important component (USFWS 2011).

Given the current problematic status of Kittlitz's Murrelet, identifying important daytime marine habitat in remote and infrequently surveyed locations will be increasingly critical for conservation efforts, particularly where such habitat may overlap with human activities. In PWS, a Murrelet concentration area hosting ~ 4% of the global population (Agler *et al*. 1998, USFWS 2013), tidewater glacier fjords are vital for Murrelet populations; during Sound-wide surveys in 2005, 2007 and 2010, an average of 87% of the Murrelets observed occurred in such fjords (range 75.8% to 97.5%; Kuletz *et al*. 2011, Cushing *et al*. 2012). Tidewater glacier fjords are also popular ecotourism destinations, an aspect that leads to substantial overlap between human use and Murrelet use areas (USFWS 2011). In turn, the high vessel traffic from ecotourism vessels can cause significant disturbance of foraging birds and potential reduction in fitness for breeding birds (Agness *et al*. 2013).

Our goal was to identify important Kittlitz's Murrelet daytime marine habitat areas within PWS that could yield the highest return for conservation and management efforts. In particular, we aimed to develop and assess a method for modeling the predicted likelihood of Murrelet daytime occurrence within 17 fjords and bays using presence-only at-sea survey data. Furthermore, we wanted to explicitly contrast Murrelet locations with the available habitat using a context-dependent modeling approach. Context-dependent modeling accounts for landscape context; it acknowledges that, among other things, an animal's interaction with its environment depends on its surroundings (Dalziel *et al*. 2008). This approach differs from context-independent analytical approaches, such as standard logistic regression of presence versus pseudo-absence data, in which pseudo-absence points are drawn randomly and not paired to use locations. Finally, we wanted to allow the available habitat to vary among used locations, and to calculate relative likelihood of occurrence for comparisons with independent survey data as a way of validating the model.

To accomplish these analysis objectives, we used a paired logistic regression modeling framework. This model is similar to a paired *t*-test, in which the values at used locations are compared with the average value of randomly sampled available points surrounding each used location. Consequently, predictor variables in the model represent the differences between used locations and the average available habitat. This approach is often more appropriate than standard logistic regression for analyzing used versus available habitat location data, as it explicitly accounts for the local variation in habitat availability that likely influences an individual's selection of habitat at any point in space and time (Breslow & Day 1980, Hosmer & Lemeshow 2000, Compton *et al*. 2002, Agresti 2002, Zeller *et al*. 2014). Overall, the methods used provide a valuable framework for analyzing presence-only data that may facilitate the delineation of important marine habitat areas in other regions and for other rare species.

METHODS

Study area

PWS is a large, glaciated embayment in south-central Alaska that includes 5 000 km^2 of shoreline waters (marine habitat within 200 m of land) and approximately 9 000 km^2 of pelagic waters (marine habitat > 200 m from land) (Fig. 1). PWS is surrounded by the Chugach National Forest, which contains 21 320 km^2 of glaciers

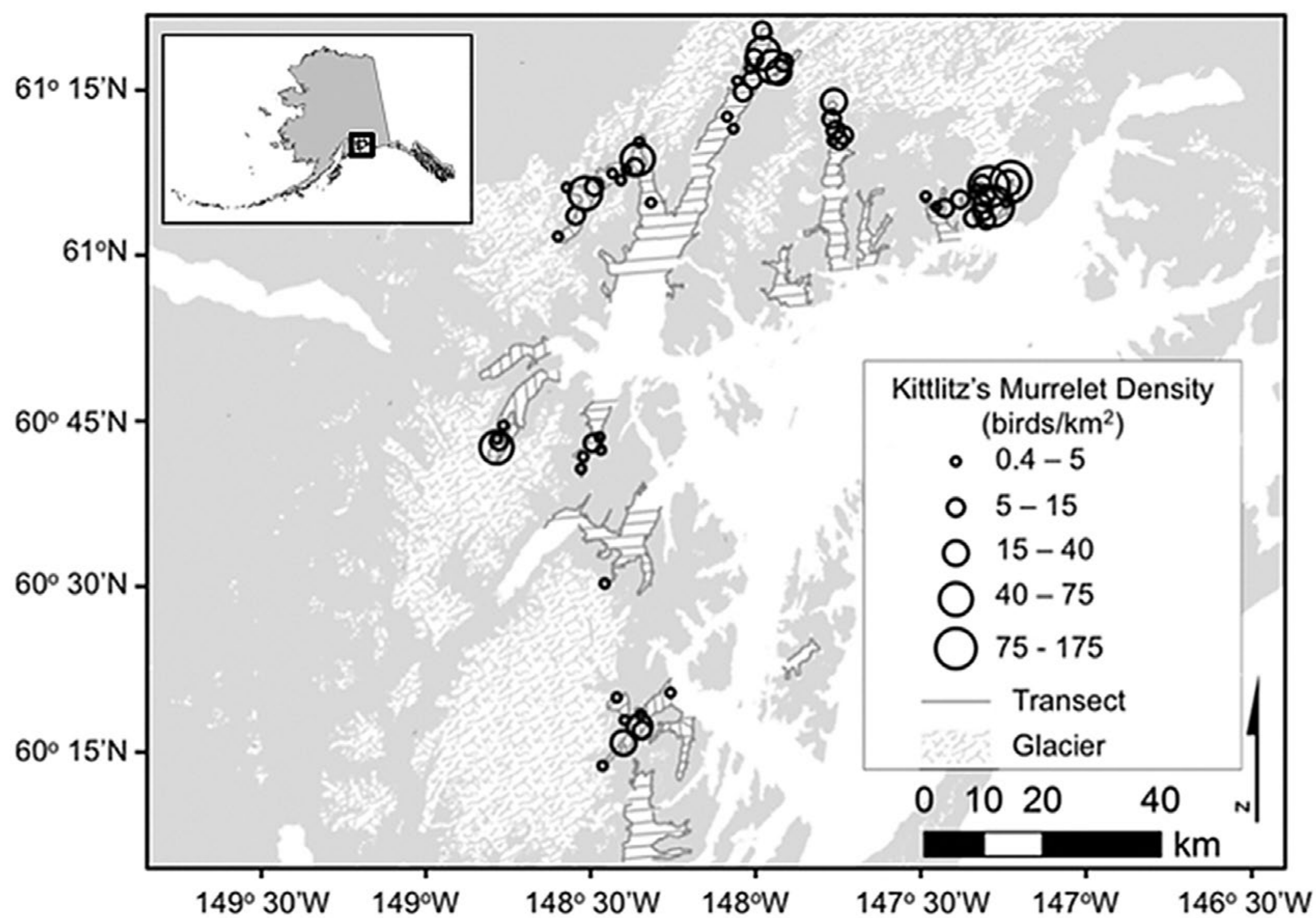

Fig. 1. Distribution and density of Kittlitz's Murrelet observed during surveys of 17 fjords and bays in Prince William Sound, Alaska, in 2009.

and ice fields (Molnia 2007). Approximately 20 tidewater glaciers terminate within PWS (Molnia 2001), providing large volumes of freshwater as well as silt and ice, particularly during summer. Depth within the glacial fjords varies from >400 m to <5 m above shallow shoals, sills and moraines. Bays without tidewater glaciers have much less depth variation, with depths typically <200m. PWS waters have a semidiurnal tidal cycle, and the weather is characterized by frequent cloud cover and precipitation (Wilson & Overland 1986).

Data collection

At-sea surveys. Between 29 June and 31 July 2009, we repeated the surveys of 17 fjords originally surveyed in 2001 to assess Kittlitz's Murrelet population size in PWS (Kuletz *et al*. 2003, 2011; Fig. 1). The 17 fjords selected in 2001 included those where Murrelets had historically been observed, as well as additional fjords that represented suitable Murrelet habitat because of similar fjord characteristics (e.g. presence of tidewater glacier) or proximity to fjords regularly used by Murrelets. Within each fjord, two observers and one boat operator surveyed the entire shoreline during a single 200 m (100 m either side and ahead of the boat) shoreline transect that circumnavigated the fjord in combination with 200 m wide parallel cross-fjord pelagic transects 1.5 or 2 km apart, depending on fjord area, in a 7 m vessel traveling at 10–15 km/h. Observers recorded all bird species using 10× binoculars. We assumed 100% detection within the 200 m wide survey strip, as observers were thoroughly trained in Murrelet identification and distance estimation. These at-sea data have been published by Kuletz *et al*. (2011) in an analysis of PWS Murrelet population trends.

We entered sighting and behavior (e.g. "floating," "foraging," "flying," etc.) data in real time onto a laptop computer running Program dLOG (Glenn Ford Consulting Inc., Portland, OR). A connected GPS unit (Garmin GPSMAP-76) stamped each sighting with geographic coordinates according to the boat's location as well as documenting the path of the survey vessel. Birds recorded in groups were assigned a single location (i.e. if we recorded a group of three birds together on the water, all had the same location). We did not include flying birds in our habitat use analysis, as we were unable to determine the exact locations where they took off or landed.

At-sea survey data from four independent sources were used to validate our Murrelet habitat use model. One of these datasets, the 2001 PWS Murrelet survey, used the same transects as our 2009 work (Kuletz *et al*. 2003). We also used the three recent USFWS summer PWS marine bird and mammal surveys (hereafter, "Sound-wide surveys") conducted in 2005, 2007 and 2010 (McKnight *et al*. 2006, 2008, Cushing *et al*. 2012). The Sound-wide survey was primarily designed to monitor seabird populations following the 1989 *Exxon Valdez* oil spill. The randomly selected transects of the Sound-wide surveys did not sample several areas with important Murrelet habitats (McKnight *et al*. 2008), such as some areas close to the face of tidewater glaciers and glacial outflow regions (Day *et al*. 2003, Kuletz *et al*. 2003). All surveys used identical survey protocols (see Kuletz *et al*. 2011).

Habitat use. We used the 2009 at-sea survey data to investigate Murrelet habitat use by distinguishing between "used" and "available" habitat. We defined used habitat as the single-point geographic location assigned to each Murrelet observation by the onboard GPS unit. In the analysis described below, our response was restricted to presence-only locations; absences were not explicitly recorded during surveys or used in the analysis. We considered treating the entire transect as the unit of observation or subdividing transects into arbitrary segments of fixed length and treating presence/absence, count or density of Murrelets as the response variable. Such analysis, however, would require subjectively deciding what classified a location as absent and how to generate absent locations, or aggregating the data into arbitrary sampling units. Therefore, we concluded that using the point locations and analyzing the data as presence-only best represented both the raw data and the survey design. We defined "available habitat" as the collection of 200 m surveyed transects, including the used habitat. We sampled the available habitat using a 100 × 100 m grid in ArcGIS v. 9.3 (ESRI 2008); we then extracted the latitude and longitude centroid for each grid cell and used these locations as our representative available habitat points.

We used Program R (R Core Development Team 2012) to calculate six spatial landscape (habitat) variables at each used and available location: 1) water depth; the shortest distance to 2) shoreline, 3) glacier, 4) moraine, and 5) freshwater streams/outflow; and 6) the presence/absence of a tidewater glacier. We created a water depth raster layer from a PWS bathymetry ASCII file (resolution: 200 m) (Kiefer *et al*. 2008). We assigned depth values for each used and available point from this bathymetry raster file using the inverse distance weighting function in the gstat package (Pebesma 2004). For the shortest distance variables, we first defined the shoreline using a data layer provided by the US Forest Service (USDA Forest Service 2008). We then used satellite images (US Geological Survey (USGS) Global Visualization Viewer Landsat Archive) from July 2009 to define the terminus position of each tidewater glacier during the survey year. Next, we used the PWS bathymetry file in combination with National Oceanic and Atmospheric Administration (NOAA) charts to identify submerged moraines as shallow (< 30 m) arms extending into and/or across fjords/bays. After that, we mapped stream locations using the same US Forest Service data layer, which included the shoreline locations. We used the shortestPath function in the gdistance package (van Etten 2011) to calculate the shortest over-water distance to each of these features. We restricted distances to the over-water distance between a point and landscape feature (glacier, moraine or outflow) by setting the land conductance value to 0 and the ocean conductance value to 1. After calculating the shortest distance to these landscape features, we then recorded the presence or absence of a tidewater glacier at each fjord using the USGS satellite images. We classified tidewater glaciers as any glacier with its terminus in the water. Fjords with tidewater glaciers are hereafter referred to as "tidewater glacial fjords" and those without tidewater glaciers are referred to as "non-tidewater glacial fjords."

Finally, we paired the habitat measures for each used point with the average values for available points within the same fjord. To do this for depth and distance variables, we first averaged all the values for each variable over all the available locations in each fjord. We then subtracted each average value from the corresponding value for each used point. For the presence/absence of a tidewater glacier variable, the average value for all fjords was calculated as the proportion of the 17 fjords surveyed that were glacial (i.e. out of the 17 fjords surveyed, 9 had tidewater glaciers; therefore, the average available habitat for the presence/absence tidewater glacier variable was 0.53). We then subtracted this proportion from the value for each used point, which was either a 1 for a bird observed within a tidewater glacial fjord or 0 for a bird observed within a non-tidewater glacial fjord. Once we calculated these variables for all observations, we had a file containing a record for every used location that included fields for differences between used and available for each of the six habitat variables.

Data analysis

Paired logistic regression habitat use model. Two different modeling approaches could be used to capture the hierarchical spatial structure of Murrelet habitat use in PWS and also to separate the two spatial scales of interest (i.e. presence and habitat use within the fjord). One approach fits models to these different scales independently (referred to hereafter as the two-stage model), while the other (referred to hereafter as the custom model) uses a custom-likelihood function to fit models to the different scales simultaneously. Here, we present the methods, results and interpretation of the two-stage model; however, the methods and results from the custom model can be found in Appendix 1 (available on the website).

Using the two-stage model, we modeled the difference in daytime marine habitat use and availability using three generalized linear models (GLMs), each with a binomial error distribution, logit link function, and no intercept term, which is a feature specific to the paired logistic regression framework (Breslow & Day 1980, Hosmer & Lemeshow 2000, Compton *et al*. 2002). Our full deterministic model for the broad-scale process of presence in a fjord was then of the form:

$$\text{Logit}(p) = \beta 1 * glacier.presence \quad (1)$$

For the finer-scale process models of habitat use within fjords, our full deterministic model for habitat use within a tidewater glacial fjord was:

$$\text{Logit}(p) = \theta_1 * depth + \theta_2 * dist.shore + \theta_3 * dist.glacier + \theta_4 * dist.moraine + \theta_5 * dist.stream \quad (2)$$

Last, our full deterministic model for habitat use within a non-tidewater glacial fjord was:

$$\text{Logit}(p) = \chi_1 * depth + \chi 2 * dist.shore + \chi_3 * dist.stream \quad (3)$$

Because of the patchy distribution of Murrelets in PWS, GLM residuals could be spatially autocorrelated. However, the relationships between residual spatial autocorrelation and parameter estimates and prediction are not clear (e.g. Ver Hoef *et al*. 2001, Schabenberger & Gotway 2005, Beale *et al*. 2007, Kissling & Carl 2008), and we are unaware of any method that can account for residual spatial autocorrelation within the paired logistic regression framework. Thus, we did not use methods to remove or account for potential residual spatial autocorrelation. Rather, we focused on examining the overall predictive ability of our habitat use model using model validation with two independent datasets.

Habitat use model evaluation and validation. We analyzed the global GLMs for the broad-scale process investigating Murrelet presence within a fjord (Eq. 1) and analyzed the two finer-scale GLMs evaluating Murrelet habitat use within tidewater glacial and non-tidewater glacial fjords (Eq. 2 and 3). Based on previous research in PWS, all of the selected spatial variables for landscape features have been shown to influence Murrelet distributions (Day *et al*. 2003, Kuletz *et al*. 2003, Stephensen 2009); therefore, *a priori* we elected to keep all variables and not to evaluate model subsets. Additionally, we examined quadratic species-environment relationships for all predictors using a presence versus pseudo-absence approach, as the paired logistic regression approach may struggle with identifying these relationships. For each used point we drew a random sample from the available habitat within the same fjord. We then visually inspected marginal and conditional plots of prediction curves and determined that the quadratic relationships were either insignificant or not ecologically meaningful. Thus, we proceeded with using the paired logistic regression model of linear terms. Finally, before examining model results, we calculated variable inflation factors (VIF) to assess potential multicollinearity among predictor variables (e.g. Neter *et al*. 1990, Chatterjee & Price 1991). All VIF values were less than 5, which is below the 5–10 or >10 thresholds used to identify potential issues of multicollinearity (Neter *et al*. 1990, Chatterjee & Price 1991, Smith & Wachob 2006).

After building the statistical models, we evaluated the model fit and validated model predictions using two independent datasets. Specifically, we evaluated the two-stage model by calculating the deviance explained for each of the three GLMs. As an additional model evaluation measure, we calculated the coefficient of concordance (CC) between observed and expected; CC ranges from -1 to 1, with a value of 1 indicating perfect agreement (Lin 1989, 2000). More specifically, CC takes into consideration both the precision and accuracy of model predictions by measuring the covariation between expected and observed values and the degree that these relationships depart from a line with a slope of 1 and y-intercept of 0 (e.g. Lin 1989, 2000, Granadeiro *et al*. 2004). Within the context of our two-stage model, the expected and observed values were the expected proportion of presences, and the observed proportion of presences across five relative probability-of-presence bins ranging from 0 to 1.

To calculate the observed and expected proportion of presences in each relative probability-of-presence bin, we followed the procedure detailed by Johnson *et al*. (2006). First, we calculated the predicted relative likelihood of occurrence (PRLO) at each 2009 Murrelet use location and all available habitat locations within tidewater glacial and non-tidewater glacial fjords (i.e. the 100 × 100 m grid of points within transect strips used to measure available habitat) using the fitted model parameters and the 2009 Murrelet data. Within tidewater glacial fjords, the PRLO was calculated by multiplying the relative likelihood of being present in the glacial fjord (Eq. 1) by the relative likelihood of being at the given location, based on its depth, distance to shore, distance to stream, distance to glacier and distance to moraine (Eq. 2). A similar process was used for calculating the PRLO within non-tidewater glacial fjords; however, the relative likelihood of being at the given location within the non-tidewater glacial fjord was a function of only depth, distance to shore and distance to stream (Eq. 3). Overall, this process resulted in two vectors: a vector of the PRLO values at all available habitat locations and a vector of the PRLO values at Murrelet use locations.

We used these two vectors to calculate the observed and expected proportions for comparison. First, the values from each of these vectors were placed into five equal-sized probability-of-presence bins ranging from 0 to 1 with breaks at 0.2, 0.4, 0.6 and 0.8. Next, we used these binned values and the midpoint of each bin to calculate the expected proportion of presences per bin, as follows:

$$\text{Expected} = ((\text{BinMid}*\text{Avail.binned.vals})/\sum(\text{BinMid}*\text{Avail.binned.vals}))*/\sum(\text{Use.binned.vals}) \qquad (4)$$

Finally, we compared observed and expected proportion of presences per bin using the CC statistic calculated by the epi.ccc function in the epiR library (Stevenson 2013). Ultimately, this procedure provides a mechanism for assessing how well model predictions, which in the paired logistic regression framework are an index of the relative likelihood of occurrence, match the true probability of presence.

We also employed CC as a model validation statistic. Similar to the evaluation procedure, we used the model parameters estimated from the model fit with the 2009 survey data to calculate the PRLO at available locations. However, for the validation procedure, these available habitat locations were not based on the 2009 survey data that were used to fit the original two-stage model. Rather, available habitat locations were generated using the transect strips from the respective validation survey dataset (i.e. the 2001 or Sound-wide surveys). In turn, the expected proportions, which use these available PRLO values, were also calculated independently for each validation dataset. Last, instead of using the 2009 survey data as the observed counts, we used each validation dataset as the observed counts. After converting these counts to proportions, each survey's observed and expected proportion of presences per bin were then used to calculate CC for that survey.

RESULTS

Abundance and distribution

In 2009, we observed a total of 680 Murrelets, 191 (2.33 birds/km^2) on pelagic transects and 489 (2.37 birds/km^2) on shoreline transects (Fig. 1). The 2009 daytime distribution of Murrelets in PWS was generally similar to the distribution documented in 2001 (see also Kuletz *et al*. 2003, 2011) using the same transects, with the exception of Columbia Bay, where we found a much higher density of Murrelets in 2009. Additionally, in 2009 we observed Murrelets in 11 of the 17 surveyed fjords. During 2001 surveys, Kuletz *et al*. (2003) had observed Murrelets in nine out of the 17 surveyed fjords.

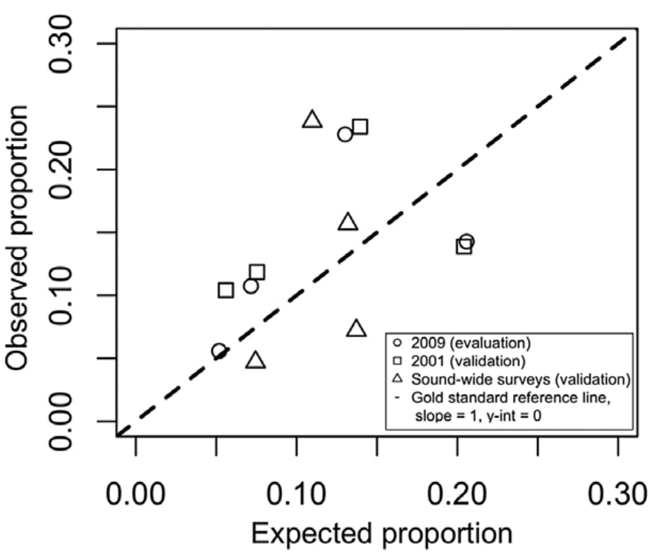

Fig. 2. Expected versus observed proportion of Kittlitz's Murrelet use occurrences calculated at five predicted relative likelihood of occurrence bins from 0 to 1, with breaks at 0.2, 0.4, 0.6 and 0.8, following methods detailed by Johnson *et al*. (2006). The expected and observed proportion data displayed here were used to calculate the concordance correlation coefficient for the 2009 data as a model evaluation measure, and the 2001 survey data and the Sound-wide survey data as model validation measures.

Habitat use

Model evaluation. All three GLMs explained a high portion of the deviance in the data. The broad-scale GLM (Eq. 1) of Murrelet presence in a fjord explained 70% ($P < 0.001$, $df = 1$) of the deviance in the presence data. Murrelets were observed within tidewater glacial fjords more than within non-tidewater glacial fjords (Table 1, model A). The GLM (Eq. 2) of Murrelet habitat use within tidewater glacial fjords explained 67% ($P < 0.001$, $df = 5$) of the deviance in the presence data. Murrelets were observed in shallow waters that were closer to shore, glaciers and moraines than the average available habitat (Table 1, model B). Last, the GLM (Eq. 3) investigating Murrelets within non-tidewater glacial fjords explained 43% ($P < 0.001$, $df = 3$) of the deviance in the presence data within non-glacial fjords. Within non-tidewater glacial fjords, Murrelets were observed closer to shore than the average available habitat (Table 1, model C). Overall, the mean CC calculated for the 2009 survey data was 0.92 (95% confidence interval [CI] 0.57–0.99), indicating a very well-calibrated model.

Model validation. CC calculated from the 2001 at-sea independent survey data (mean 0.85, 95% CI 0.46–0.95) and the Sound-wide independent survey data (mean 0.91, 95% CI 0.39–0.99) suggest the two-stage model had considerable predictive ability. This substantial correlation between expected and observed proportions (Fig. 2) is also reflected by the general overlap between Murrelet use locations from the different datasets and locations of high PRLO values (Figs. 3-6). However, there were a few areas where observations and corresponding PRLO values did not match well. For example, in Port Bainbridge no Murrelets were observed during the surveys, yet PRLO values from the model predictions were very

TABLE 1
Parameter estimates of three generalized linear models describing Kittlitz's Murrelet presence or habitat use in Prince William Sound, Alaska, 2009

Model	Parameter	Estimate[a]
A: presence within 17 fjords and bays	Glacier (Presence/Absence)	6.04
B: habitat use within tidewater glacial fjords	Depth	0.02
	Distance to shore	-3.86
	Distance to stream	0.87
	Distance to glacier	-0.51
	Distance to moraine	-0.47
C: habitat use within non-tidewater glacial fjords	Depth	-0.04
	Distance to shore	-9.42
	Distance to stream	-0.77

[a] Standard errors and probability values are not reported, given the potential sensitivity of these inferences to residual spatial autocorrelation.

high in some locations (~ >0.8) (Fig. 3). In contrast, PRLO values were very low in parts of upper Unakwik Inlet, upper College Fjord and Harriman Fjord (~ <0.3), where considerable numbers of Murrelets were observed during 2001 surveys and Sound-wide surveys (Fig. 5b, 5c).

DISCUSSION

Habitat model framework and evaluation

We proposed and tested a technique for identifying important daytime Murrelet habitat areas in PWS using presence-only at-sea survey data and spatial geographic information system (GIS) data. Although there are many different approaches to modeling presence-only species data (for a review see Pearce & Boyce 2006), a context-dependent modeling approach based on paired logistic regression (that is, case-controlled logistic regression and conditional logistic regression) best met our analysis objectives for several reasons. Generally, paired logistic regression is a simple and effective way to model context-dependent habitat selection (Agresti 2002). More specifically, paired logistic regression allows us to define the available habitat differently for unique use location points and entirely avoids the issue of sample contamination. Contamination can occur because used locations are often excluded if the location is also in the pseudo-absence sample (e.g. Manly *et al*. 2002). Other approaches, such as MaxEnt (Elith *et al*. 2011), are unable to deal with this situation and require a single fixed landscape to be defined to represent the available habitat for all used locations (Phillips *et al*. 2006, Elith *et al*. 2011). This flexibility was deemed critical because observations of radio-tagged Murrelets suggest they have relatively high fjord-site fidelity (unpub. data). In turn, although different fjords may be theoretically available, we were interested in selection among available habitat locations within the fjord where an individual was observed. Next, other approaches would have calculated a different response variable than predicted relative likelihood of occurrence (e.g. Ecological Niche Factor Analysis — habitat suitability indices [Hirzel *et al*. 2002]). This would have restricted our ability to evaluate model predictions based on used locations from independent datasets.

Our analysis of Murrelet habitat use supports previous research in PWS, suggesting that Murrelets use fjords with tidewater glaciers more than non-tidewater glacial fjord habitats (Kuletz *et al*. 2011). Within tidewater glacial fjords, our results agree with past

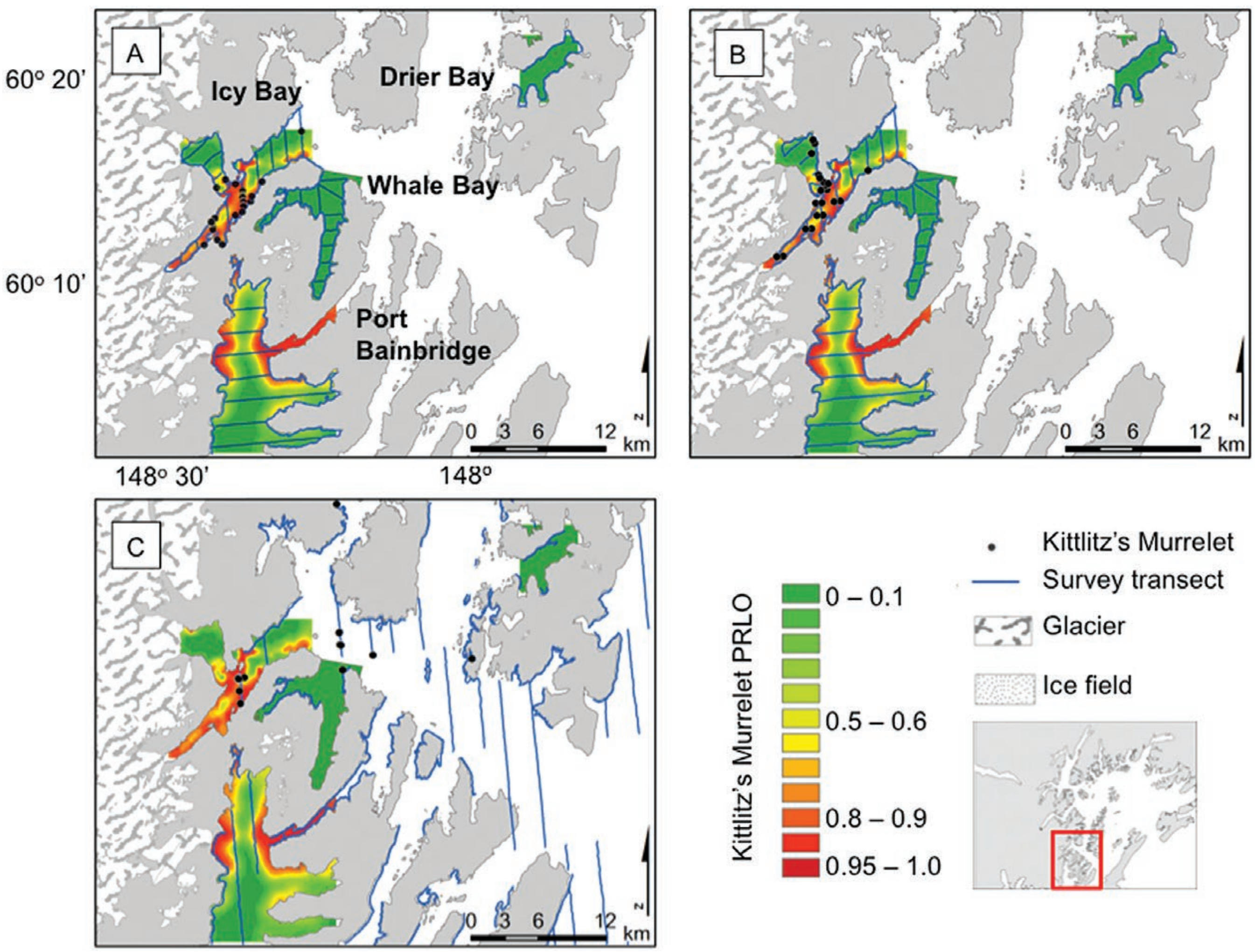

Fig. 3. Kittlitz's Murrelet observations (black circles) from 2009 surveys used in model creation (A), independent intensive surveys in 2001 (B), and independent Sound-wide surveys (2005, 2007, 2010) (C) in southern PWS, overlaid on Kittlitz's Murrelet relative likelihood of occurrence prediction surface, which was calculated from the model describing Kittlitz's Murrelet relative likelihood of occurrence as a function of water depth, distance to shore, and distance to glacier.

investigations indicating that Murrelets use shallow habitats closer to shore, glaciers and moraines (Day *et al*. 2003, Stephensen 2009). Within non-tidewater glacial fjords, Murrelets also appeared to use habitats that were closer to shore. However, unlike previous efforts, we used our habitat use models to quantitatively predict the relative likelihood of Murrelet occurrence across all surveyed fjords, and we used independent datasets to validate the model's predictive ability.

Model validation and ecological interpretation

Overall, the high CC values for both the 2001 at-sea survey data and the Sound-wide surveys show that our two-stage model performs well and has strong predictive ability. Moreover, the model is robust. In particular, the two datasets we used to validate our model were designed with different objectives. While the 2001 survey specifically targeted Murrelet habitat, the Sound-wide surveys were designed to sample a more diverse set of habitats and species. Consequently, the spatial arrangement of transects were different between the two surveys. However, our model appears to be robust to the potential spatial biases introduced by these different survey designs, as both surveys yielded high CC.

The PRLO maps overlaid with Murrelet use locations for the different surveys reveal additional interesting patterns. Generally, Murrelet locations overlap areas with the highest PRLO values, as we would expect, given the good model fit and high CC. Furthermore, our model appears to capture both "typical" distributions and distributions occurring during two occurrences of abnormally dense aggregations (i.e. fjords where we observed considerably higher numbers of Murrelets than had been historically observed during PWS Sound-wide surveys), one in Heather Bay during the summer of 2007 (Allyn *et al*. 2008) and one in Columbia Bay during the summer of 2009. Although these aggregations had not been previously documented in either bay, in both cases they occurred in areas with the highest PRLO values.

In a few fjords, predictions did not match Murrelet observations well: either PRLO values were high in regions where Murrelets were not observed (sections of Port Bainbridge), or PRLO values were low in areas where Murrelets were observed (sections of upper Unakwik Inlet, upper College Fjord and Harriman Fjord). This disparity between predictions and survey observations suggest that factors outside the modeled habitat variables are affecting

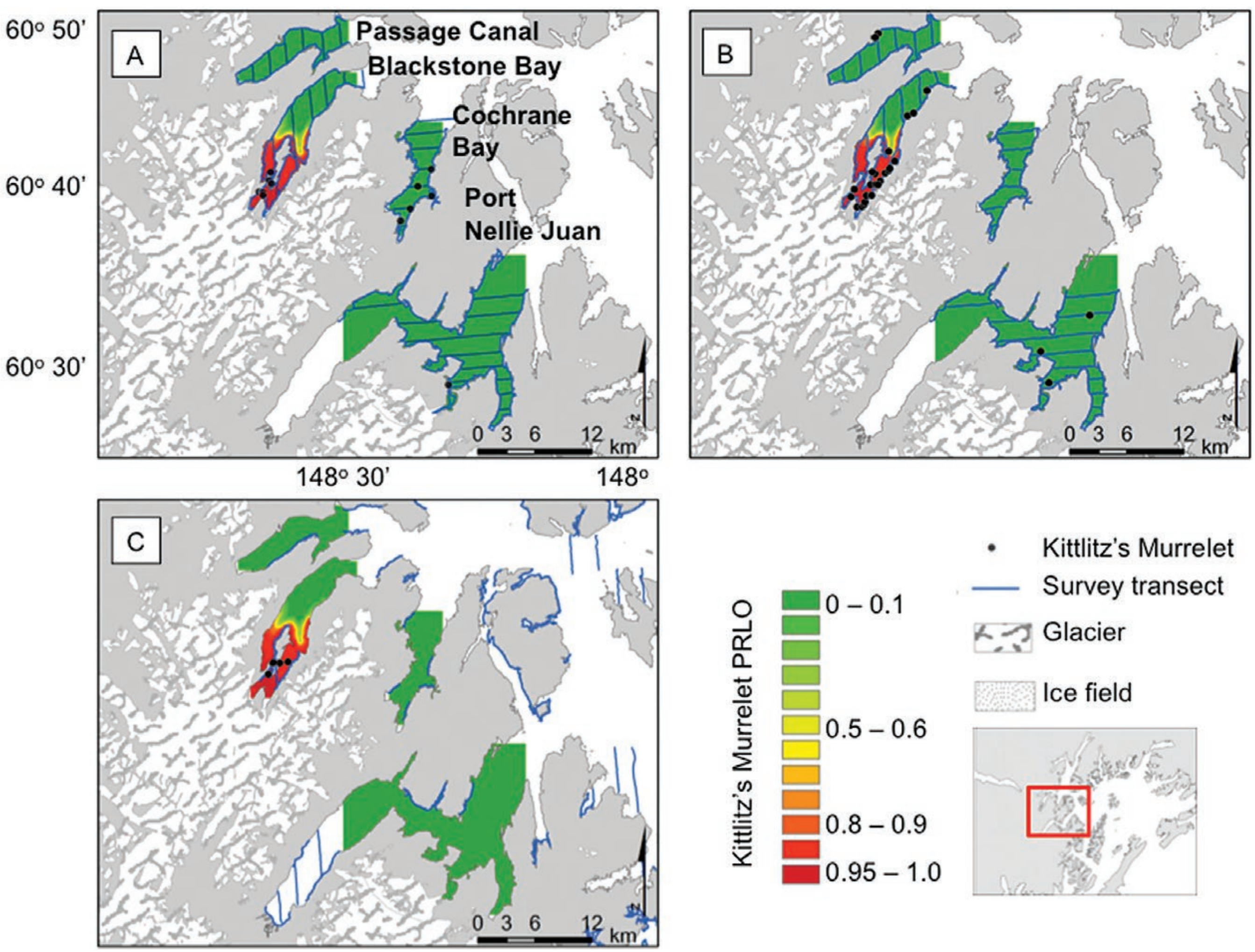

Fig. 4. Kittlitz's Murrelet observations (black circles) from 2009 surveys used in model creation (A), independent intensive surveys in 2001 (B), and independent Sound-wide surveys (2005, 2007, 2010) (C) in central PWS, overlaid on Kittlitz's Murrelet relative likelihood of occurrence prediction surface, which was calculated from the model describing Kittlitz's Murrelet relative likelihood of occurrence as a function of water depth, distance to shore, and distance to glacier.

the habitat quality in these areas. Port Bainbridge is unique in its degree of exposure; it opens directly into the Gulf of Alaska, and it is therefore subject to oceanographic influences very different from the mainland/northern fjords in PWS. Interestingly, however, earlier USFWS surveys (e.g. in 1993 and 2004) did record a few Murrelets in Port Bainbridge, all within high PRLO regions (Kuletz *et al*. 2011).

The disagreements between model predictions and survey observations may also be linked to tidewater glacier characteristics. For example, in Port Bainbridge the glacier terminates in the intertidal zone, which might affect habitat quality. The link between tidewater glacier status and habitat quality appears even stronger for fjords in northwest PWS where PRLO values were low and many Murrelets were observed (Fig. 5). Specifically, the tidewater glaciers in upper College Fjord and upper Unakwik Inlet are advancing and the Harriman Glacier is stable (Molnia 2010). In contrast, most other PWS tidewater glaciers are retreating.

Glacier status (e.g. stable, advancing or retreating), and glacier characteristics (e.g. depth at terminus and size) can have profound influences on the local fjord ecosystem. Specifically, these traits drive calving rates, sedimentation levels and freshwater influx within the fjord system (Post 1975, Koppes & Hallet 2002). These processes, in turn, can affect the physical characteristics of the water column, altering the distribution and composition of biological communities (Dierssen *et al*. 2002, Etherington *et al*. 2007). In particular, waters flowing under the tidewater glaciers and into the fjord can increase nutrient concentrations and promote high levels of productivity near the face of the tidewater glacier (Apollonio 1973). Additionally, the influx of cold, fresh water may cause osmotic shock and stun invertebrate zooplankton and forage fish prey (Hartley & Fisher 1936, Scott 1936, Weslawski & Legezynska 1998, Zajaczkowski & Legezynska 2001), which would then float to the surface where foraging Murrelets could easily capture them. Indeed, these tidewater glacier fronts have been shown to be hotspots for other seabird species in other regions (Brown 1980, McLaren & Renaud 1982, Lydersen *et al*. 2014). Of course, linking Murrelet distributions to these mechanisms would require additional model variables not captured by the habitat variables used in our models (e.g. Arimitsu *et al*. 2012). Overall, however, it does seem that the status and characteristics of these tidewater glacier fjords allow Murrelets to

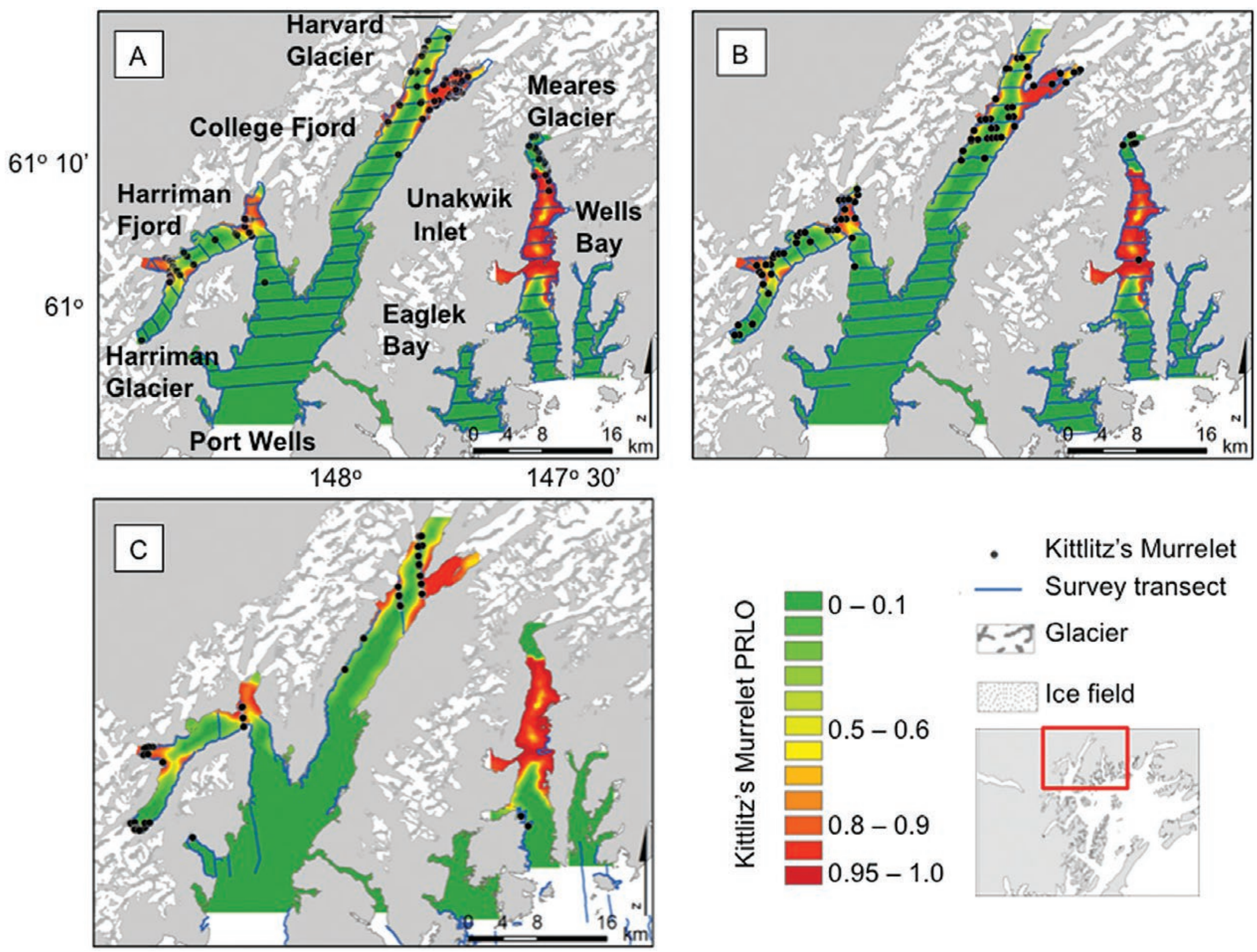

Fig. 5. Kittlitz's Murrelet observations (black circles) from 2009 surveys used in model creation (A), independent intensive surveys in 2001 (B), and independent Sound-wide surveys (2005, 2007, 2010) (C) in northwestern PWS, overlaid on Kittlitz's Murrelet relative likelihood of occurrence prediction surface, which was calculated from the model describing Kittlitz's Murrelet relative likelihood of occurrence as a function of water depth, distance to shore, and distance to glacier.

exploit these habitats although these locations have relatively low PRLO values. Alternatively, these disparities may simply reflect the overall low numbers of Murrelets in PWS and the consequent inability of birds to use all available habitats with high PRLO values.

Research and management implications

An important consideration regarding our presence-only modeling framework, and specifically its application to other geographic areas or species, is how we defined available habitat. Delineating available habitat and how it will be compared to use locations (i.e. one definition of available constant for all use points, or available habitat varying among use points) determines the habitat variable values that are then fit with the GLM. Consequently, estimated parameters and eventual conclusions are all highly sensitive to how available habitat is defined (Zeller *et al*. 2014). Broadly, the available habitat should capture the range of environmental conditions available to the species; however, this needs to be modified by the spatial characteristics of the survey conducted to collect the use data. In particular, any potential spatial biases inherent in the collection of the use data should also be accounted for when selecting the available habitat locations (Phillips *et al*. 2009). Doing so prevents comparisons of use data with available data collected from locations representing unique environmental conditions not encountered during the survey. For our study, we accomplished this by using the survey transect strips as the available habitat. Any potential spatial bias in the use data was therefore shared by the available habitat data. Once the available habitat has been defined, another issue is how to compare the available habitat with the use locations. In our study, individual fjords represented meaningful spatial and ecological units for comparison because Murrelets in PWS appear to show high fjord-site fidelity (unpub. data). However, any application of this modeling framework for Murrelets in different regions or other species would require careful consideration of how to delineate the available habitat and how to compare the available habitat with the use data.

Given a well-justified definition of available habitat, the paired logistic regression modeling framework could provide many benefits to research and monitoring programs. Specifically, for animals with small population sizes, one of the primary goals is detecting changes in abundance. This generally requires some

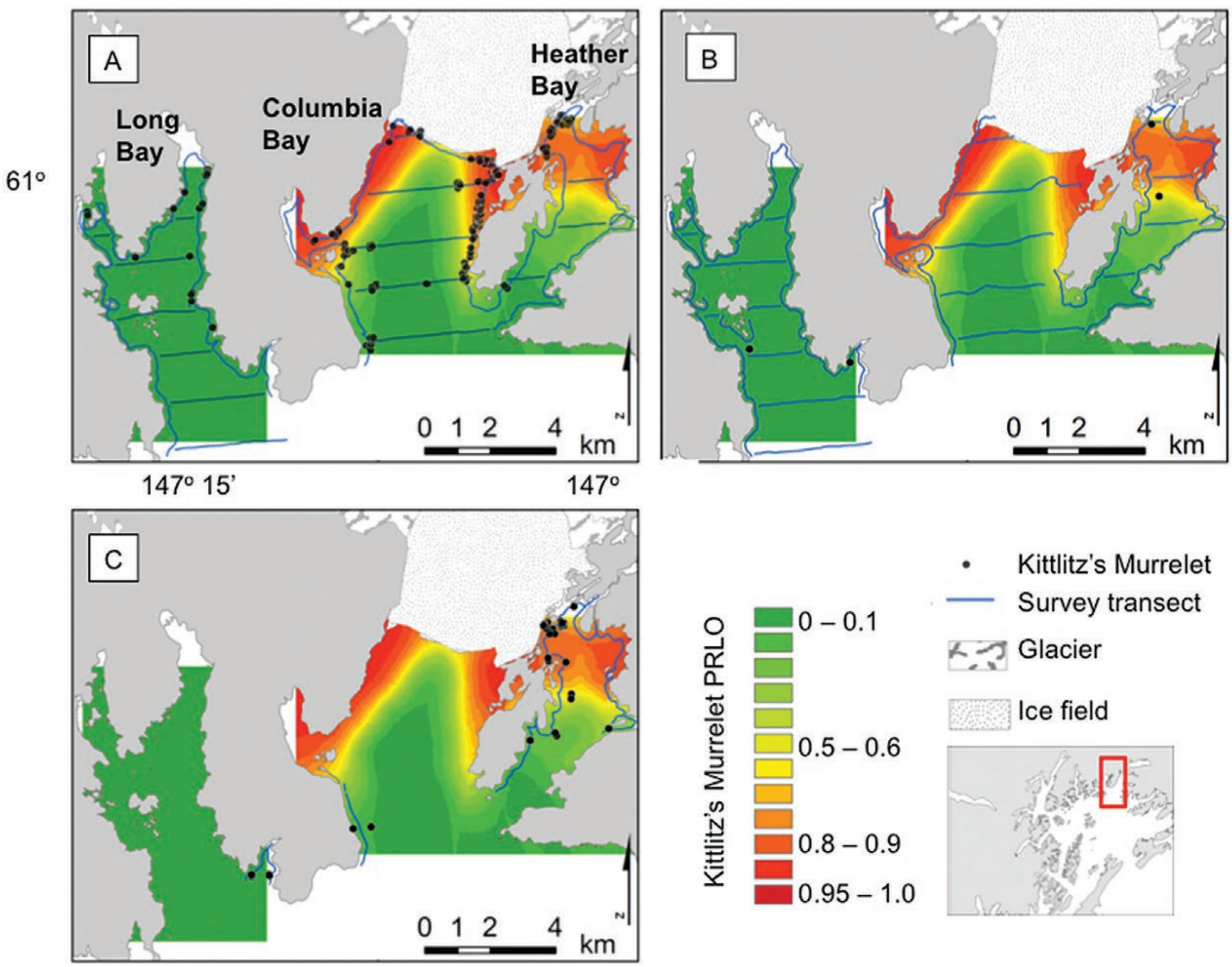

Fig. 6. Kittlitz's Murrelet observations (black circles) from 2009 surveys used in model creation (A), independent intensive surveys in 2001 (B), and independent Sound-wide surveys (2005, 2007, 2010) (C) in northeastern PWS, overlaid on Kittlitz's Murrelet relative likelihood of occurrence prediction surface, which was calculated from the model describing Kittlitz's Murrelet relative likelihood of occurrence as a function of water depth, distance to shore, and distance to glacier.

type of survey. In the case of Murrelets, these surveys are mainly done at sea, where the spatial variation among individuals may significantly influence our ability to uncover population trends (Kissling *et al*. 2007). Accurately identifying such spatial patterns using the paired logistic regression modeling framework may help stratify at-sea surveys by delineating high and low relative probability of use areas. In turn, the habitat use maps could guide survey efforts, increasing our ability to detect population changes while maximizing limited monitoring resources. Notably, within these systems the habitat use patterns of Murrelets are influenced by complicated mechanisms not included in our model, including oceanographic characteristics (Allyn *et al*. 2012) and the distribution of prey (Arimitsu *et al*. 2012). Therefore, future efforts should strive to include these variables as well in the paired logistic regression model, as they will likely increase the predictive ability of models and the accuracy of habitat use maps.

Conservation efforts for rare, elusive species with home ranges in remote locations, such as Kittlitz's Murrelet, present numerous logistic and economic challenges. For Murrelets, these challenges are intensified by the overlap between Murrelet habitat and human use areas, especially in such popular tourist destinations such as tidewater glacial fjords in PWS, Glacier Bay and Kenai Fjords, Alaska. In PWS during the recent Sound-wide surveys (2005, 2007 and 2010), an average of 87% of Murrelet observations were within such fjords. We suggest that our approach is a useful tool that can be applied to delineate important daytime marine habitat areas within these fjords. For example, PRLO values could be used to determine overlap between certain human activities and important Murrelet habitats, or, if necessary, to delineate zones for additional management, while limiting overall effects on commercial and recreational activities.

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