# Using Ships of Opportunity to Assess Winter Habitat Associations of Seabirds in Subarctic Coastal Alaska

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## Abstract

In subarctic waters winter may be the period during which seabirds face the greatest environmental and physiological pressures, yet seabird distribution during this time is poorly understood. Using at-sea surveys conducted in Prince William Sound, Alaska on research 'ships of opportunity' from November 2007 to March 2009, we investigated how seabird abundance and distribution vary within and between winters for three common seabird species with extensive ranges: common murre *(Uria aalge)*, marbled murrelet (*Brachyramphus marmoratus*), and black-legged kittiwake (*Rissa tridactyla*). Due to a large proportion of zeros in the survey data, hurdle models were performed using generalized additive mixed models. Across the two winters, consistent temporal patterns in density and distribution were observed for all species. Common murre and marbled murrelet both increased in number in midwinter, while black-legged kittiwake decreased to very low numbers. Habitat association models revealed that common murre favored relatively protected waters while marbled murrelet favored inside bays and passages (which make up 45% of semi-protected waters) and areas of higher sea surface temperatures. Our results suggest that winter storms influenced seabird distribution, particularly in midwinter when temperatures were lowest and storms more frequent. This influence was greater than variables providing proxies for foraging opportunities, which were absent from selected models. Our study highlights the importance of considering species-specific temporal patterns throughout the non-breeding season to guide marine spatial planning that will fully address seabird conservation issues.

**Keywords**: Prince William Sound, *Brachyramphus marmoratus*, *Uria aalge, Rissa tridactyla*, non-breeding season

## Introduction

Seabird populations can be impacted by pollution events (Peterson et al. 2003), direct and indirect interactions with fisheries (Tasker et al. 2000, Okes et al. 2009), and increasingly through marine environmental change (Pichegru et al. 2010). Many species of seabird are currently under pressure from some and in many cases all of these threats. Improving our understanding of marine habitat requirements for seabirds can help predict the impacts of events and assist in the selection of appropriate marine protected areas (Hooker and

Gerber 2004, Amorim et al. 2009). Because most seabird studies occur during the summer breeding season, little is known about winter habitat requirements.

Winter may be the period during which seabirds face the greatest environmental pressures and competition for food can be high (Lack 1968, Hunt et al. 2005). For those species at higher latitudes that do not migrate great distances, food tends to be relatively scarce or relatively inaccessible, the climate more extreme, light levels reduced, day length shorter, and water temperatures colder. Consequently, daily energy requirements increase (Fort et al. 2009) and birds have to forage for a large proportion of reduced daylight hours (Daunt et al. 2006). Wind and sea state are known to affect surface-feeding seabirds in particular (Dunn

1973, Taylor 1983) but diving birds can also be impacted and the effects of weather conditions on survival have been observed in common murre (*Uria aalge*) and European shag (*Phalacrocorax aristotelis;* Harris and Wanless 1996, Piatt and Van Pelt 1997, Frederiksen et al. 2008). In response to these environmental challenges, seabirds may perform large-scale movements during winter and may aggregate in areas where high bird densities can be sustained for a limited period (Vaitkus 2001). Spatial distribution of seabirds during winter can be characterized by a high degree of patchiness rather than an even dispersal (Skov et al. 2000, Garthe et al. 2009). Therefore discrete aggregations can occur at which large proportions of a geographic population may be found (Skov et al. 1995, Petersen et al. 1999).

During the nonbreeding season a number of seabird species feed upon a wider variety of prey than they do during summer (Shealer 2002). Sanger (1987) found that common murre and marbled murrelet (*Brachyramphus marmoratus*) in southcentral Alaska fed on a variety of prey items in winter, and Ouwehand et al. (2004) recorded a varied winter diet in common murre in the North Sea. Black-legged kittiwakes (*Rissa tridactyla*) exploit a wider range of food sources in winter than they do in summer, including, in the Atlantic, increased amounts of discards and offal (Camphuysen et al. 1995). Therefore, studying single predator-prey associations during the nonbreeding season may not yield strong results, because seabirds may congregate in areas with predictable concentrations of a variety of prey items based on benthic habitat, bathymetry, or exposure to the elements (Hunt et al. 1999, Weimerskirch 2007, Garthe et al. 2009). Seabirds have been shown to associate with physical and biological ocean processes (Decker and Hunt 1994, Weichler et al. 2004, Ainley et al. 2005, Hyrenbach et al. 2006, Yen et al. 2006, Garthe et al. 2009) as well as with specific bathymetric features (Yen et al. 2004, Amorim et al. 2009). Such environmental factors may be better predictors of seabird distribution than prey abundance (Ainley et al. 2004).

In this study we describe changes in abundance and distribution through the winter period for

three seabird species that overwinter in Prince William Sound (PWS), a large fjord-type estuary in subarctic waters of southcentral Alaska: common murre, marbled murrelet, and black-legged kittiwake. All three species have extensive ranges and are abundant in PWS, with estimated March 2005 populations of approximately 91,000 common murre, 16,000 black-legged kittiwake and 9,000 marbled murrelet (McKnight et al. 2006). We further investigate fine scale habitat associations (1 km$^{-2}$) for two of the three species, as black-legged kittiwake were not recorded with sufficient frequency to enable statistical analysis. We investigate how habitat associations change through the winter for common murre and marbled murrelet and discuss the possible causes of temporal variation. Finally, we examine the implications of our findings for incorporation of biodiversity data into marine spatial planning and establishment of protected areas at sea.

## Methods

### Study Area

Prince William Sound is part of coastal south-central Alaska, primarily between 60° and 61° N, and is separated from the adjacent Gulf of Alaska (GOA) by large, mountainous islands (Figure 1). The coastline is rugged and extensive and includes many fjords, bays, and islands. Bays and fjords are diverse, with average depths ranging from < 50 m (typically referred to as bays) to > 400 m (typically fjords). Outside the bays and fjords are basins and passages of varying depths down to 700 m. There are several large icefields and more than 20 tidewater glaciers (Molnia 2001).

Annual precipitation can be as high as 5.4 m. Winter months from October through March are characterized by high storm frequencies (Wilson and Overland 1986). Abundant rain, snow, and glacial melt result in a strong cyclonic circulation that generally travels east to west (Niebauer et al. 1994). During summer the waters of PWS are highly stratified, but during winter months they are more mixed, with GOA surface waters pulsing into PWS via the Alaska Coastal Current (ACC; Niebauer et al. 1994). The northern half of PWS is strongly influenced by glacial runoff
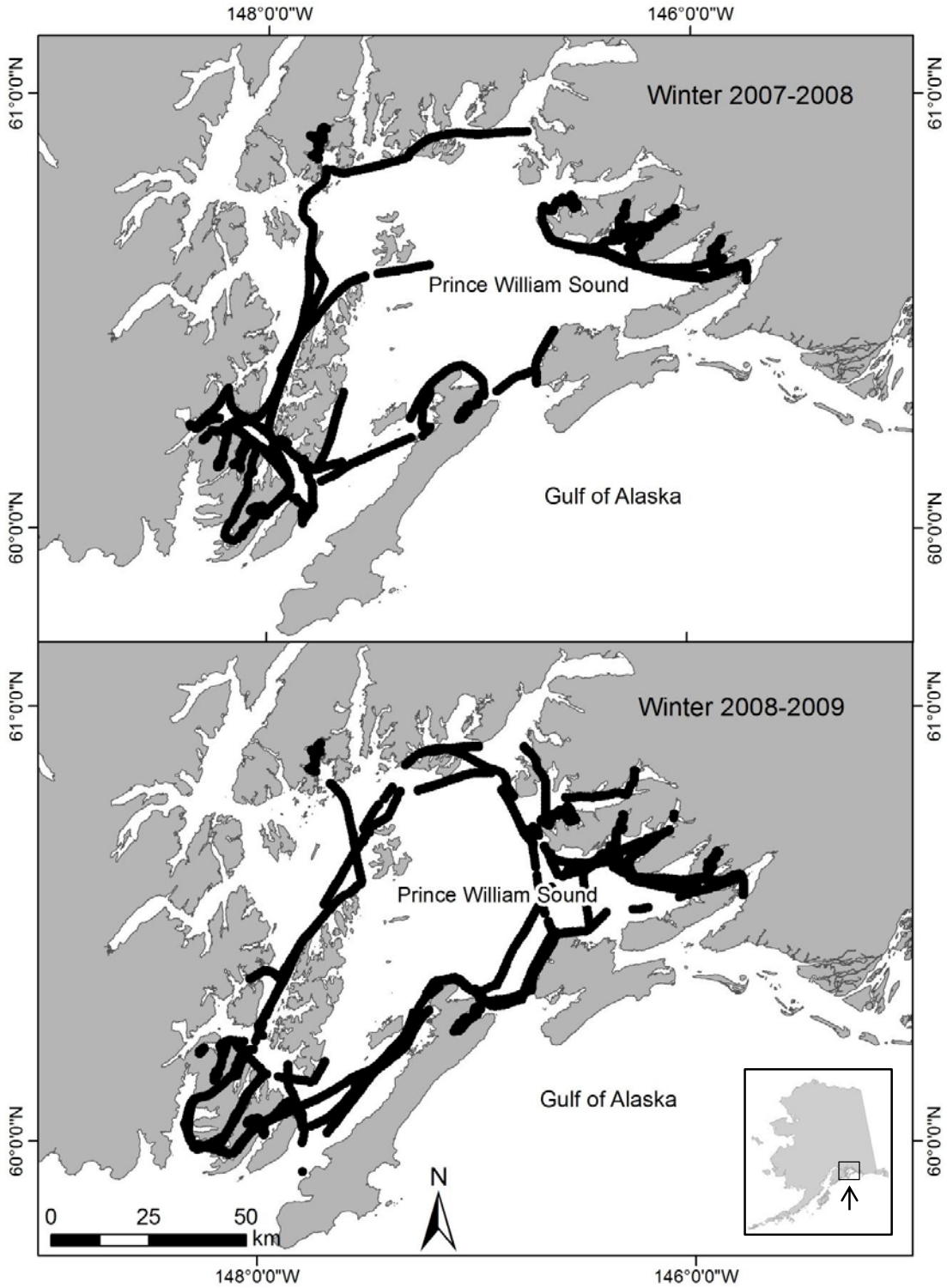
Figure 1. Map of Prince William Sound with survey tracks by winter season, November 2007– March 2009.

in the fjords and tends to be colder and fresher relative to the ACC-influenced waters that are warmer and more saline (Wang et al. 2001). Sea surface temperatures in the fjords can be as low as 1 °C in late winter, with some inner bays and fjords choked with ice (Gay and Vaughan 2001).

The fish assemblage of PWS is diverse, but is dominated in biomass by Pacific herring (*Clupea pallasii*), Pacific cod (*Gadus macrocephalus*), walleye pollock (*Gadus chalcogrammus*) and various salmonids (genus *Oncorhynchus*) (Willette et al. 1997). Other fish species important to seabirds include Pacific sand lance (*Ammodytes hexapterus*) and capelin (*Mallotus villosus*) (Kuletz et al. 1997; Anthony et al. 2000; Suryan et al. 2000, 2002). Herring spawn from late March through early May (Bishop and Green 2001, Norcross et al. 2001), a major event which may provide concentrations of food for various seabirds in the pre-breeding season.

## Survey Methods

Our seabird surveys were one component of a series of integrated projects aimed to investigate factors limiting recovery of Pacific herring in PWS. In order to conduct our surveys, we relied on research ships chartered for conducting hydroacoustic surveys for juvenile herring and for censusing humpback whale (*Megaptera novaeangliae*). Despite the challenge of reduced spatial and temporal data consistency associated with surveys from ships of opportunity, our methods for analyzing our survey data could be applied to studies with similar platforms of opportunity. Further, because winter distribution and habitat associations of seabirds are poorly understood, the temporal patterns and habitat associations examined provide important additions to current knowledge.

We conducted eight surveys of seabirds in PWS in November, January and March over two winters, 2007/08 and 2008/09. Surveys undertaken were: 05–12 and 24–29 November 2007 (292 and 137 km surveyed, respectively), 23–28 January 2008 (246 km), 12–19 March 2008 (419 km), 6–13 November 2008 (200 km), 23–28 January 2009 (250 km), 4–9 and 18–25 March 2009 (221 and

518 km, respectively), totaling 2283 km. Seabird observations were conducted using established U.S. Fish and Wildlife Service (USFWS) protocols (USFWS 2007), except that flying birds were counted continuously rather than using intermittent scans, following protocols for small boat surveys in PWS (USFWS 2002). One experienced observer using 10x binoculars recorded number of birds occurring within a strip transect width of 300 m (150 m both sides and ahead of the boat), being careful not to double count birds following the boat. All birds within the strip were counted continuously and their individual behavior recorded (on water, flying, foraging). All surveys were carried out using the same 17 m charter vessel with a clear observation platform 2.5 m above sea level. Surveys were only conducted while traveling on a direct course at a constant speed of between 3 and 9 knots. The observer recorded observations directly into a laptop computer integrated with a global positioning system (GPS) using the program dLOG (R.G. Ford Consulting, Portland OR). The GPS-integrated program provided location data at 20-sec intervals and for every entered observation.

Detection probability can change across weather and sea conditions (Hyrenbach et al. 2007, Barbraud and Thiebot 2009, Ronconi and Burger 2009), particularly for small and/or cryptically colored birds (Mack et al. 2002, Spear et al. 2004). The waters of PWS are relatively well protected with little swell, which provided good, calm survey conditions. Of the 2283 km surveyed, 94% were conducted in Beaufort scale 0–2, 5% in Beaufort scale 3, and 1% in Beaufort scale 4 sea state. Our methodology minimized variance in detectability by only counting birds within 150 m of the boat under accepted sea state and visibility conditions. The observer recorded a descriptive variable of his perceived ability to detect birds in prevailing weather conditions (Tasker et al. 1984, Veit et al. 1993, Speckmann 2004, Sydeman et al. 2009); observations were omitted if visibility was considered compromised within 200 m of the vessel. Because we applied the same protocol in both years, we assumed the error due to detectability was equally distributed among areas and surveys. Consistent with Fauchald et al. (2011), we recognize that the small bodied murrelets may

TABLE 1. List of variables determined for each survey 1 km$^{-2}$ midpoint.

| Covariate | Category | Description |
|---|---|---|
| Tr | Factor | 1-km$^{-2}$ transect name, $n = 2283$ |
| Mar | Factor | Marine habitat type, $n = 4$ |
| Exp | Factor | Wave exposure category, $n = 3$ |
| Distland | Continuous | Distance to closest land (m) |
| Depth | Factor | Depth category, $n = 4$ |
| Slope | Continuous | Slope of seabed (°) |
| Sub | Factor | Substrate category, $n = 3$ |
| Distkelp | Continuous | Distance to closest kelp bed (m) |
| Disteel | Continuous | Distance to closest eelgrass bed (m) |
| SST | Continuous | Monthly mean sea surface temp in 10 km$^{-2}$ grid (°C ), $n = 233$ |
| Winter | Factor | November–March period, $n = 2$ |
| Moyr | Factor | Month/year of cruise, $n = 6$ |
| Lat | Continuous | Latitude at km$^{-2}$ midpoint |
| Long | Continuous | Longitude at km$^{-2}$ midpoint |

have been underestimated, and present the density estimates as relative values.

## A-priori Designation of Explanatory Variables

Data were obtained for a number of environmental variables, based on biological rationales supporting their ability to explain seabird distribution outside the breeding season (Table 1). Because data representing spatial and temporal variation in the abundance of prey species within PWS during winter is absent, particularly at appropriate scales, we used variables providing proxies for foraging opportunities. Using geographic information system (GIS) software (ArcMap 9.2), we spatially matched explanatory variables to survey data, taking values at the midpoint of each 1 km transect, thus building a detailed profile of each kilometer of survey trackline. For continuous variables we also calculated the range, mean, and standard error (SE; Table 2).

Marine habitat was included as a variable to capture seabird use of different areas for foraging or shelter during winter months. Selected marine habitat categories were: within bay (685 of 2283 km surveyed), mouth of bay or passage (254 km surveyed), within passage (297 km surveyed) and open water (1047 km surveyed). Within bay

TABLE 2. Variable summaries demonstrating the seabird habitat surveyed in Prince William Sound.

| Variable | Range | Mean ± SE |
|---|---|---|
| Distland (m) | 8 – 9952 | 1557 ± 28 |
| Disteel (m) | 28 – 13509 | 2298 ± 44 |
| Distkelp (m) | 34 – 70921 | 23609 ± 404 |
| SST (C°) | -1 – +8 | 4 ± 0.1 |
| Slope (°) | 0 – 28 | 3 ± 0.1 |

reflects areas inside the mouth of an enclosed bay. The mouth of bays and passages refers to the area between two headlands and approximately 1 km in either direction; these are areas where tidal and estuarine fronts often occur and concentrate potential prey species (Gay and Vaughn 2001), however, detailed data on the occurrence of these fronts were unavailable. Passage refers only to narrower passes measured as < 3 km wide in GIS. Passages > 3 km wide were categorized as open water.

Winter weather events have the potential to influence seabird distribution (Vaitkus 2001). We used wave exposure of the nearest point of land to indicate whether birds seek less turbulent waters during winter and if this habitat choice varied among winter months. Exposure was taken from National Oceanic and Atmospheric Administration (NOAA) ShoreZone coastal inventory and

mapping project (NOAA 2010*a*). Categories included exposed/semi-exposed (570 out of 2283 km), semi-protected (1444 km) and protected (269 km) waters. Points > 3 km from shore were classified as semi-exposed waters.

Distance to shore was included as a variable because many juvenile fish are found in greater concentrations in nearshore environments (Beck et al. 2003) and freshwater runoff may also create nutrient-rich fronts (Gay and Vaughn 2001). The distance to shore was taken from the center point of each kilometer surveyed. Depth was included also because fish assemblages tend to vary by depth gradient (Johnson et al. 2008) and additionally because different seabird species are restricted by their diving capabilities. Depth (in meters) was obtained from the Alaska Ocean Observing System (2010) grid of bathymetry for PWS that is modeled to a resolution of 500 m. Slope was included because bathymetric features can influence upwelling and thereby provide feeding opportunities for marine predators like seabirds (Yen et al. 2004). Slope is the angle of seabed in degrees, determined from GIS calculations based on the Alaska Ocean Observing System bathymetry grid.

Fish assemblages may differ strongly with substrate (Hamilton and Konar 2007). Details of substrate type were obtained from the ShoreZone coastal inventory and mapping project (NOAA 2010*a*) and included three categories: rock (455 out of 2283 km), rock and sediment (849 km) or sediment (979 km, including gravel, sand and mud). Eelgrass beds (*Zostera marina*) and kelp beds (primarily *Nereocystis luetkeana*, *Agarum clathratum* and *Lamanaria saccharina*), occur in specific areas of PWS, and are associated with high productivity as well as providing protection and food for a variety of juvenile fish (Dean et al. 2000, Johnson et al. 2010). Locations of coastal kelp and eelgrass beds were also obtained from the ShoreZone project (NOAA 2010*a*) and distance to them in meters calculated using GIS.

Sea surface temperature (SST), which may influence both prey availability (Abookire and Piatt 2005) and seabird energetic requirements (Daunt et al. 2006), was obtained from the National

Aeronautics and Space Administration (NASA) Giovanni website (Goddard Earth Sciences Data and Information Services Center 2009), which provides monthly SST averages obtained from satellites for points in a 10 km grid. The resulting grid provided 233 points with SST measurements in PWS at each time point. Temporal variables included winter (whether winter 2007/08 or 2008/09) and month/year (combination of month and winter), which were included to account for possible changes in density seasonally and between winters.

## Data Exploration

We explored seasonal changes in abundance and distribution for the three seabird species that were the most consistently abundant during our avian surveys, have substantial breeding populations in PWS, and occur across large geographic areas in the northern hemisphere: common murre, a deep-diving alcid, black-legged kittiwake, a medium-sized surface feeder and marbled murrelet, a small, diving alcid which is globally endangered (IUCN 2010). These three species were selected from 19 marine bird species regularly recorded.

Following the protocol outlined in Zuur et al. (2010), we carried out data exploration to look for outliers, zero inflation (when there are too many zero observations), collinearity, and to investigate the type of relationships between birds and covariates. We plotted the spatial position of the sampling sites to visualize the consistency of sampling sites over time. Cleveland dotplots indicated no extreme outliers but showed that values for the variable depth were not sampled along an equal-spaced gradient. We therefore converted depth into a categorical variable for each 1 km transect: 0–50 m ($n = 612$ km), 50–100 m ($n = 665$ km), 100–150 m ($n = 320$ km), > 150 m ($n = 686$ km).

Frequency plots were used to assess the proportion of zeros in the data and for each species the number of non-zero observations per transect kilometer was calculated. The species with the most non-zero observations out of 2283 total km surveyed was common murre ($n = 751$). For other species the numbers of non-zero observations were: murrelet 343 and kittiwake 198. Kittiwakes had

so few positive observations, particularly during midwinter, that the data were not suitable for modeling habitat association.

Collinearity between covariates was investigated using pairplots (multi-panel scatterplots) and variance inflation factors (VIF). Pairplots only capture two-way relationships whereas VIF detect high-dimensional collinearity (Zuur et al. 2010). Covariation was assessed using the threshold of 0.4 for correlation coefficient and 3 for VIF. Based on pairplots, distance to kelp beds and latitude (Pearson correlation, $r = 0.5$), distance to shore and distance to eelgrass ($r = 0.5$), and, depth and slope ($r = -0.4$) were determined to be collinear and therefore none of these combinations of covariates were used in the same model. Exploring VIFs showed the following pair combinations to be collinear: month/year and SST; ocean habitat category and distance to eelgrass; and, SST and winter. As may be expected when modeling complex habitat associations for highly mobile species, scatterplots for both presence-absence and presence-only data for each species showed that only weak patterns could be expected. This provides an extra reason to deal with even the smallest amount of collinearity as it may confound the estimates of effect.

Seabird surveys were conducted from ships of opportunity undertaking fish and marine mammal research, and although cruises covered similar areas, the locations of the sampled transects were not identical over time (Figure 1). Preliminary data exploration found a transect effect and a cruise effect, with observations made on the same 1 km transect and cruise being more closely related than otherwise. Due to the opportunistic nature of surveys, interpretation of temporal trends between survey periods (November, January and March) was confounded with minor changes in spatial position of the sampling sites. For this reason, latitude and longitude were included as explanatory variables to reveal any strong spatial bias in seabird density, occurrence, or geographical pattern to bird distribution. The large range covered during each survey (minimum 137 km and a maximum of 518 km) provided a broad range of data across each variable (see explanatory variables section),

which served to limit the influence of any spatial bias on statistical results for habitat association.

## Statistical Analyses

We calculated density (birds km$^{-2}$) of each seabird species for each kilometer of survey trackline. The seabird distribution data contained a large proportion of zero observations for all three focal species. The zero observations were considered to be true zeros and not undetected birds. Therefore hurdle models were applied whereby data are analyzed initially as presence-absence with all zeros included and positive observations coded as one, followed by a separate analysis of presence-only data, excluding all of the zero observations (Boucher and Guillén 2009, Zuur et al. 2009). The first analysis attempted to determine which covariates were driving the presence and absence of birds, while the second analyses focused on the question of which covariates were driving the density of birds when they were present. All models were run using the R version 2.11 (R Development Core Team 2008) and associated mgcv package (Wood 2004).

For the presence-absence data a binomial generalized additive mixed model (GAMM) was used with transect as a random intercept. This ensured that a correlation structure was imposed on the observations from the same 1 km transect. Observations from different transects were assumed to be independent as they were temporally and spatially distinct.

For the presence-only data we used a GAMM with a gamma distribution suitable for density data, with transect as a random intercept. For a detailed description of the statistical methods see Zuur et al. (2012). We used an Information Theoretic approach (Burnham and Anderson 2002), defining 15 models *a priori* separately for each species, which we then compared using Akaike Information Criterion (AIC) weights. There is some evidence to suggest that weakly significant variables ($P > 0.01$) should not be considered when using GAMMs (Wood 2006) and therefore we only investigated highly significant relationships ($P < 0.01$). We performed post-hoc testing with Bonferroni corrections to show specifically

which category of nominal variables was key to significant relationships contained in the models. We present all means ± SE.

## Results

### Seabird Densities

Common murre were the most frequently observed of the three species overall and individually for every survey period, with the exception of November 2007, when marbled murrelet were recorded in slightly higher densities (Figures 2 and 3, Table 3). Marbled murrelet were the next most commonly recorded species. Kittiwakes remained relatively scarce throughout the winter months with only two of the six time periods (March 2008 and November 2009) showing densities > 1.0 birds km$^{-2}$ (Figure 4).

For all three species consistent temporal patterns in population density were detected between November, January and March. Common murre increased in density between November and January both years (Figure 2 displays winter 2007/08). Marbled murrelet also increased in density from early to midwinter, peaking in January then decreasing as winter progressed (Figure 3, Table 3). In contrast, in both winters kittiwakes occurred in negligible densities during January surveys (<0.01 and 0.04 birds km$^{-2}$; Table 3), decreasing from November and then increasing again in March (Figure 4). All three species were present in higher densities in March 2008 compared to March 2009 (Table 3).

### Habitat Associations

*Common Murre* – For presence-absence data the models SST, SST + exposure, and month/year were the preferred models (Table 4), and collectively > 98% of the Akaike weights were attributable to these three models. However, for both model 2 (SST) and model 11 (SST+ exposure) none of the variables had $P$-values ≤ 0.05. The only model with a significant estimated parameter was model 1 (month/year), for which month/year was highly significant ($P < 0.001$), largely due to lower murre density in November 2007 than during all other surveys.
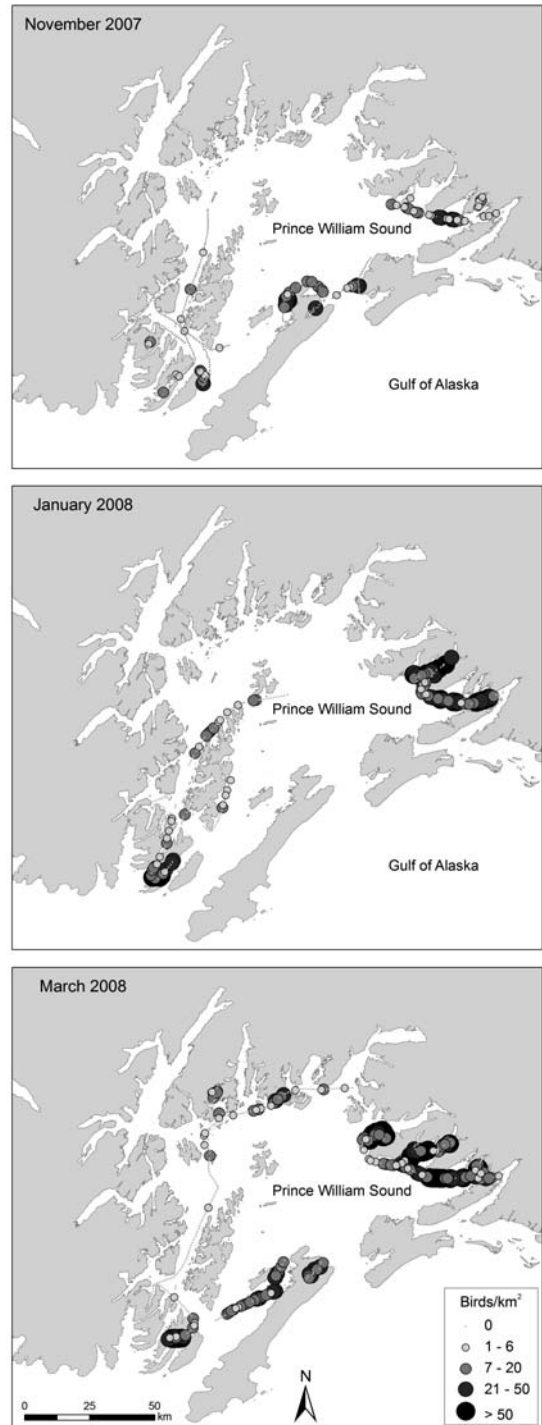


Figure 2. Densities and distributions of common murre in Prince William Sound Alaska during 2007–2008 winter surveys. Densities are expressed as the number of individuals sighted per square kilometer.
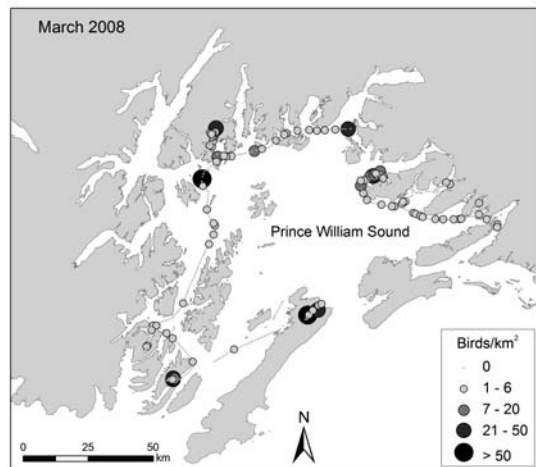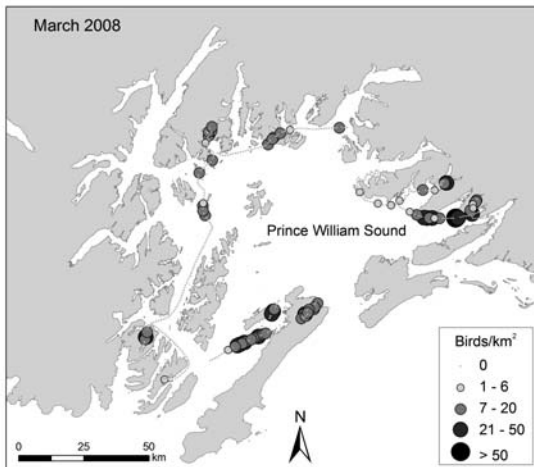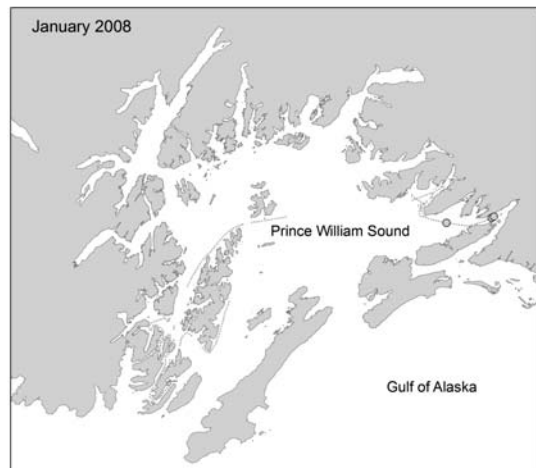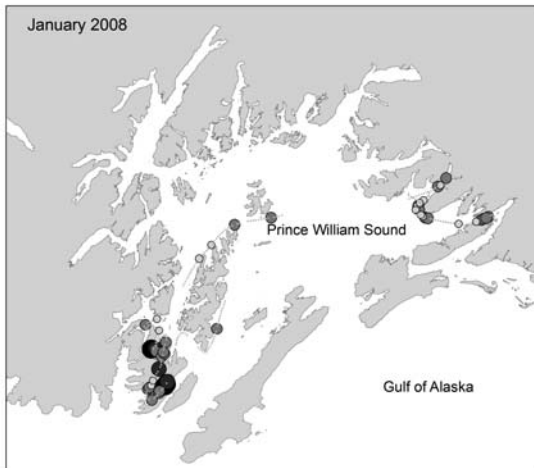
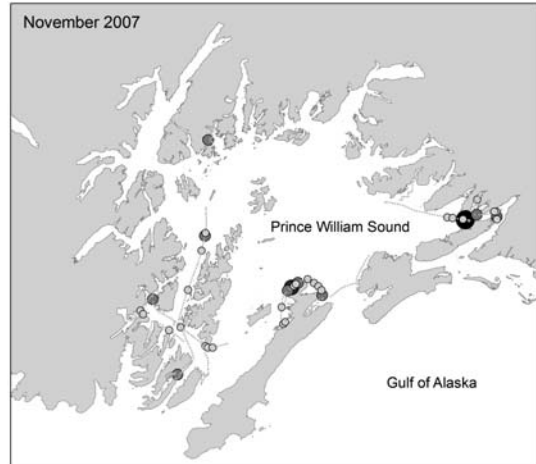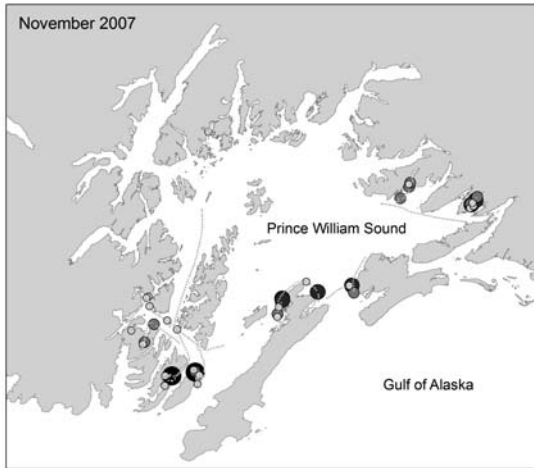Figure 3. Densities and distributions of marbled murrelet in Prince William Sound Alaska during 2007–2008 winter surveys. Densities are expressed as the number of individuals sighted per square kilometer.

Figure 4. Densities and distributions of black-legged kittiwake in Prince William Sound Alaska during 2007–2008 winter surveys. Densities are expressed as the number of individuals sighted per square kilometer.

TABLE 3. Mean (SE) densities (birds km$^{-2}$) of three seabird species in Prince William Sound during two consecutive winters.

| Species | Winter | Nov | Jan | Mar |
|---|---|---|---|---|
| Common murre | 2007/08 | 1.7 (0.3) | 11.7 (2.2) | 19.4 (2.8) |
| | 2008/09 | 3.9 (0.5) | 14.9 (3.2) | 11.2 (3.0) |
| Marbled murrelet | 2007/08 | 2.0 (0.4) | 4.4 (2.3) | 2.4 (0.3) |
| | 2008/09 | 3.0 (0.5) | 5.5 (1.7) | 0.8 (0.1) |
| Black-legged kittiwake | 2007/08 | 0.6 (0.2) | 0.04 (0.0) | 2.4 (0.5) |
| | 2008/09 | 1.9 (0.6) | 0.01 (0.0) | 0.1 (0.0) |

TABLE 4. Estimated Akaike's information criterion (AIC$_c$) and values, changes in AIC, and Akaike weights for hurdle models for common murre data, based on presence-absence and presence-only per 1 km$^{-2}$ transect. No statistics are present for those models that failed to converge.

| Model | Model description* | Presence-absence† | | | Model | Presence-only‡ | | |
|---|---|---|---|---|---|---|---|---|
| | | AIC$_c$ | ΔAIC | $\omega_i$ | | AIC$_c$ | ΔAIC | $\omega_t$ |
| M2 | s(SST) | 10757.7 | 0.0 | **0.83** | M5B | 2539.6 | 0.0 | **1.00** |
| M1 | fMoyr | 10762.1 | 4.4 | **0.09** | M7B | 2574.3 | 34.7 | 0.00 |
| M11 | s(SST) + fExp | 10763.0 | 5.3 | **0.06** | M7 | 2580.3 | 40.7 | 0.00 |
| M13 | s(Slope) + fSub | 10766.9 | 9.2 | 0.01 | M9 | 2581.3 | 41.7 | 0.00 |
| M5 | fExp +fMoyr | 10767.0 | 9.3 | 0.01 | M11 | 2583.3 | 43.7 | 0.00 |
| M3 | fMar + fMoyr | 10780.6 | 22.8 | 0.00 | M11B | 2594.4 | 54.8 | 0.00 |
| M10 | s(Disteel) + s(SST) | 10784.2 | 26.5 | 0.00 | M6 | 2595.1 | 55.5 | 0.00 |
| M11B | s(SST) + fExp + f_Exp(SST) | 10785.7 | 27.9 | 0.00 | M12B | 2614.6 | 75.0 | 0.00 |
| M4 | s(Slope)+ fMar + fMoyr | 10790.8 | 33.1 | 0.00 | M13B | 2641.7 | 102.1 | 0.00 |
| M8 | s(Lat) +s(Long) + fMoyr | 10808.0 | 50.3 | 0.00 | M14B | 2674.83 | 135.2 | 0.00 |
| M5B | fExp +fMoyr + f(Exp,Moyr) | 10820.2 | 62.4 | 0.00 | M5 | 2694.2 | 154.6 | 0.00 |
| M7 | s(Distland) + fExp + fWinter | 10821.2 | 63.5 | 0.00 | M8B | 2702.3 | 162.7 | 0.00 |
| M3B | fMar + fMoyr + f(Mar, Moyr) | 10822.4 | 64.7 | 0.00 | M2 | 2710.3 | 170.7 | 0.00 |
| M7B | s(Distland) + fExp + fWinter + f(Exp,Winter) | 10826.0 | 68.3 | 0.00 | M3 | 2717.0 | 177.4 | 0.00 |
| M12B | s(Distland) + s(SST) + f(Distland, SST) | 10831.0 | 73.3 | 0.00 | M14 | 2723.0 | 183.4 | 0.00 |
| M15 | s(Distland) +s(Slope)+ fSub | 10833.0 | 75.2 | 0.00 | M13 | 2724.6 | 185.0 | 0.00 |
| M6 | s(Distland) + fMoyr | 10847.9 | 90.2 | 0.00 | M8 | 2727.3 | 187.7 | 0.00 |
| M8B | s(Lat) +s(Long) + fMoyr + f(Lat, Long) + f_Moyr(Lat) + f_Moyr(Long) | 10880.5 | 122.8 | 0.00 | M15 | 2730.6 | 191.0 | 0.00 |
| M14 | fDepth + fMar | 10892.0 | 134.6 | 0.00 | M4 | 2736.9 | 197.3 | 0.00 |
| M14B | fDepth + fMar + f(Depth, Mar) | 10967.6 | 209.8 | 0.00 | M15B | 2741.5 | 201.9 | 0.00 |
| M9 | s(Lat) +s(Long) +s(SST) + fMar | - | - | - | M1 | 2741.8 | 202.2 | 0.00 |
| M12 | s(Distland) + s(SST) | - | - | - | M3B | 2853.4 | 313.8 | 0.00 |
| M13B | s(Slope) + fSub + f (Slope,Sub) | - | - | - | M10 | - | - | - |
| M15B | s(Distland) +s(Slope)+ fSub + f_Sub(Distland) | - | - | - | M12 | - | - | |

†for presence-absence data, a binomial generalized additive mixed model (GAMM) was used.
‡ for presence-only data, a GAMM with a gamma distribution was used. All models incorporated Transect as a random intercept.
* s( ) represents a smoothing function; f represents function of.

For common murre presence-only data, month/ year + exposure (model 5b) had the lowest AIC (Table 4), with a significant interaction ($P < 0.01$). This model also accounted for 100% of the Akaike weight ($\omega_i$). Post-hoc testing with Bonferroni corrections found that greater densities of common murre occurred in protected and semi-protected waters ($P < 0.01$). Across all surveys this equated to an average density of 38 murres km$^{-2}$ in protected and semi-protected waters ($n =$ 595 positive observations) compared to a density of 9 murres km$^{-2}$ in exposed and semi-exposed waters ($n = 156$ positive observations).

*Marbled Murrelet* – For marbled murrelet presence-absence data, model 11 (latitude + longitude + SST + marine habitat) was the best model with lowest AIC (Table 5). In this model marine habitat was significant ($P < 0.005$) as was SST ($P < 0.01$), whereas latitude and longitude were not ($P > 0.9$).

TABLE 5. Estimated Akaike's information criterion (AIC$_c$) values, changes in AIC, and Akaike weights for hurdle models for marbled murrelet presence-absence data and presence-only data per 1 km$^{-2}$ transect. No statistics are presented for those models that failed to converge.

| Model | Model description* | Presence-absence† | | | Model | Presence-only‡ | | |
|---|---|---|---|---|---|---|---|---|
| | | AIC$_c$ | ΔAIC | $\omega_i$ | | AIC$_c$ | ΔAIC | $\omega_i$ |
| M11 | $s$(Lat) + $s$(Long) +$s$(SST) + $f$Mar | 11737.8 | 0.0 | **1.00** | M15B | 1028.1 | 0.0 | **1.00** |
| M3B | $s$(Distland) + $s$(SST) + $f$(Distland,SST) | 11763.6 | 25.8 | 0.00 | M7B | 1122.5 | 94.4 | 0.00 |
| M1 | $f$Moyr | 11765.1 | 27.3 | 0.00 | M13B | 1137.8 | 109.7 | 0.00 |
| M3 | $s$(Distland) + $s$(SST) | 11765.6 | 27.8 | 0.00 | M14B | 1138.0 | 109.9 | 0.00 |
| M8 | $f$Exp + $f$Moyr | 11775.0 | 37.2 | 0.00 | M4B | 1146.4 | 118.3 | 0.00 |
| M9 | $s$(SST) + $s$(Distland) + $f$Exp + $f$Mar | 11775.8 | 38.0 | 0.00 | M6B | 1173.0 | 145.0 | 0.00 |
| M4 | $f$Mar + $f$Moyr | 11776.5 | 38.7 | 0.00 | M6 | 1183.8 | 155.7 | 0.00 |
| M12 | $s$(Disteel) + $s$(SST) | 11782.9 | 45.1 | 0.00 | M12 | 1196.4 | 168.3 | 0.00 |
| M7 | $s$(Slope)+ $f$Mar + $f$Moyr | 11786.5 | 48.7 | 0.00 | M9 | 1196.5 | 168.4 | 0.00 |
| M6 | $s$(Distland) + $s$(Slope) + $f$Sub | 11787.5 | 49.7 | 0.00 | M3B | 1197.5 | 169.4 | 0.00 |
| M5 | $s$(Distland) + $f$Moyr | 11803.2 | 65.4 | 0.00 | M3 | 1199.5 | 171.4 | 0.00 |
| M8B | $f$Exp + $f$Moyr + $f$(Exp, Moyr) | 11804.6 | 66.9 | 0.00 | M14 | 1200.5 | 172.4 | 0.00 |
| M6B | $s$(Distland) + $s$(Slope)+ $f$Sub + $f$_Sub(Distland) | 11810.1 | 72.3 | 0.00 | M15 | 1202.7 | 174.6 | 0.00 |
| M14 | $s$(Disteel) + $f$Sub + $f$Moyr | 11824.6 | 86.8 | 0.00 | M5 | 1223.5 | 195.4 | 0.00 |
| M4B | $f$Mar + $f$Moyr + $f$(Mar,Moyr) | 11860.5 | 122.7 | 0.00 | M7 | 1228.0 | 199.9 | 0.00 |
| M2 | $f$Depth | 11867.1 | 129.3 | 0.00 | M2 | 1232.3 | 204.2 | 0.00 |
| M7B | $s$(Slope)+ $f$Mar + $f$Moyr + $f$(Mar,Moyr) | 11871.7 | 133.9 | 0.00 | M13 | 1232.6 | 204.5 | 0.00 |
| M13 | $f$Depth + $f$Mar | 11873.4 | 135.7 | 0.00 | M1 | 1253.8 | 225.7 | 0.00 |
| M15 | $s$(Distland) + $f$Mar + $f$Depth + $f$Sub + $f$Moyr | 11932.5 | 194.7 | 0.00 | M8 | 1256.8 | 228.7 | 0.00 |
| M13B | $f$Depth + $f$Mar + $f$(Depth, Mar) | 11937.2 | 199.4 | 0.00 | M4 | 1262.9 | 234.9 | 0.00 |
| M5B | $s$(Distland) + $f$Moyr + $f$_Moyr(Distland) | 11950.7 | 212.9 | 0.00 | M11 | 1271.8 | 243.7 | 0.00 |
| M10B | $s$(Lat) + $s$(Long) + $f$Moyr + $f$(Lat,Long) + $f$_Moyr(Lat) + $f$_Moyr(Long) | 12017.2 | 279.4 | 0.00 | M8B | 1277.0 | 248.9 | 0.00 |
| M15B | $s$(Distland) + $f$Mar + $f$Depth + $f$Sub + $f$Moyr + $f$(Mar,Sub) +$f$(Sub,Moyr) | 12149.7 | 411.9 | 0.00 | M10B | 1284.2 | 256.1 | 0.00 |
| M10 | $s$(Lat) + $s$(Long) + $f$Moyr | - | - | - | M10 | 1286.2 | 258.1 | 0.00 |
| M11B | $s$(Lat) + $s$(Long) + $s$(SST) + $f$Mar +$f$_Mar(SST) | - | - | - | M11B | 1300.1 | 272.0 | 0.00 |
| M14B | $s$(Disteel) + $f$Sub + $f$Moyr + $f$_Moyr(Disteel) + $f$(Sub,Moyr) | - | - | - | M5B | - | - | - |

†for presence-absence data, a binomial generalized additive mixed model (GAMM) was used.
‡ for presence-only data, a GAMM with a gamma distribution was used. All models incorporated Transect as a random intercept.
* $s$( ) represents a smoothing function; $f$ represents function of.

The SST effect was linear and positive, indicating that birds were more likely to be present in warmer surface waters. Post-hoc testing with Bonferroni corrections revealed that marbled murrelets were also significantly more likely to be encountered in either bays or passages than in open water ($P < 0.01$). In addition, the probability of encountering birds within bays (19% or $n = 185$ out of 982 km of transect) was significantly greater ($P < 0.01$) than in waters at the mouths of bays and passages or in open water (12% or $n = 138$ out of 1301 km of transect). The high murrelet densities within bays were particularly evident in January of both years (Figure 3), when the probability of encountering birds on a km transect rose to 29% (54 out of 185 observations).

For marbled murrelet presence-only data, model 15B (distance to shore + marine habitat + depth + substrate + month/year with interactions) was the best fit, with lowest AIC (Table 5) and accounted for 100% of the Akaike weight. The interaction between substrate and month/year was highly significant ($P < 0.001$). The post-hoc tests revealed that high densities of marbled murrelets were encountered in areas with substrates consisting of sediment (gravel, sand, mud) or mixed rock and sediment, rather than areas with a purely rocky substrate. Average density of murrelets in areas with a rocky substrate was 9.7 birds km$^{-2}$ ($n = 58$ positive observations out of 456 km) as opposed to average density of 17.4 murrelets km$^{-2}$ in areas with substrate consisting of sediment or rock and sediment ($n = 285$ positive observations out of 1827 km). The difference was considerably higher in January when 28.9 marbled murrelets km$^{-2}$ were observed in areas with substrate consisting of sediment or rock and sediment ($n = 78$ positive observations out of 401 km), and only 10.4 birds km$^{-2}$ in areas with rocky substrate ($n = 20$ positive observations out of 95 km).

## Discussion

Our surveys are the first to be conducted for seabirds in PWS during winter months other than March. The survey data collected were extensive, with more than 2200 km of observations recorded across a variety of environmental gradients. Due to the opportunistic nature of our surveys there were slight spatial inconsistencies in transects between survey periods, and the surveyed areas did not cover the entire PWS. Therefore, the results of the surveys are not intended to accurately estimate population sizes, but do reveal previously unpublished trends in abundance and distribution of three common seabird species throughout the winter period. Additionally, the species-specific consistency of distribution patterns between the two study years for marbled murrelets, common murres, and black-legged kittiwakes substantiate that the patterns we observed were not spurious. Results clearly show that seasonal patterns differed markedly among the three study species, suggesting that winter seabird assemblages must be disaggregated to species or species group level for impact evaluation and conservation purposes. For all three seabird species, seasonal patterns in densities were consistent for both winters. Kittiwakes were nearly absent from PWS in midwinter whereas densities of the two diving species increased at this time.

Our habitat modeling approach allowed us to examine possible reasons for changes in winter distribution of different seabird species. Results demonstrate that environmental variables used in the models are useful indicators of potential overwintering habitat for seabirds and reveal drivers of habitat selection. Our survey design was opportunistic rather than systematic, but our modeling approach sought to mitigate some of these limitations and provided new information about seabird habitat associations during a seasonal period for which such information is exceedingly scarce. Further systematic seabird surveys in PWS and spatial modeling, ideally incorporating data on tidal and estuarine fronts as well as improved variables representing prey availability may elaborate and clarify the relationships uncovered in this study.

Our results suggest that distribution of both common murre and marbled murrelet may be influenced by winter climate. We found a close association between common murre and protected waters in midwinter. During winter, PWS provides far more sheltered waters than the adjacent GOA

and we observed highest densities in protected waters during January in both winters. Winter wrecks of common murre have been recorded in the northern GOA, including PWS (Piatt and Van Pelt 1997) and rough seas can negatively impact foraging behavior for common murre in other regions (Finney et al. 1999). Winter storms in the GOA peak from December to February at which time average wind strength is highest, air temperature lowest, and wave height greatest (Stabeno et al. 2004, NOAA 2010*b*). Schroeder (2007) found that the strongest winds in the adjacent GOA waters occur near the outer coast of PWS with winds at their strongest and coldest in January and February. We observed opposing trends in seasonal common murre density in PWS relative to those observed in the GOA by Day (2006), which suggests that the less exposed waters of PWS provide refugia during winter for this species.

We found that the probability of encountering marbled murrelets during the nonbreeding season was positively related to SST. Marbled murrelets can dive and acquire food at up to 50 m depth, although most of their foraging occurs in the upper 25 m of the water column (Burger 1991, Jodice and Collopy 1999). Diving can be metabolically expensive in colder sea temperatures due to increased heat loss (Kooyman et al. 1976, Gremillet et al. 1998). Surface waters in PWS are coldest in March (average 2.88 °C in 2008 and 2.54 °C in 2009; Vaughan et al. 2001) while in the GOA, average March SST is comparatively warm, at 5.5 °C. This marked difference in SST inside vs. outside PWS could explain the late-winter decline in marbled murrelet numbers in PWS and the high densities (for pelagic waters) of murrelets recorded during March in the GOA by Day (2006). The association of marbled murrelets with SST and their occurrence in bays and passages may indicate the extremity of winter climatic factors influences murrelet distribution, similar to the effect of wave exposure on common murre distribution. Murres and murrelets are closely related and ecologically similar, thus the need to conserve energy by avoiding resting or foraging in exposed seas under extreme winter conditions may be a priority for both species.

While bays and passages are typically sheltered from storms, they are also important overwintering habitat for seabird prey. In particular, high densities of juvenile Pacific herring overwinter in relatively shallow bays within PWS (Stokesbury et al. 2000, Thorne 2010), where they would be accessible to murrelets. In January, we found highest densities of murrelets in areas with non-rocky substrates. Such habitats support a variety of potential murrelet prey such as juvenile fish and forage fish species (Hamilton and Konar 2007, Thorne 2010) and possibly marine invertebrates, which murrelets also consume in winter and spring (Sanger 1987, Nelson 1997).

The changes observed in distribution of the subsurface foraging murres and murrelets throughout winter were strikingly different than those observed for surface foraging kittiwakes. Kittiwakes have been recorded as abundant at the end of winter in March (McKnight et al. 2006), but little is known about population trends in the preceding months, and we had insufficient sightings of them during midwinter to conduct detailed habitat association analyses. Kittiwakes are medium-sized surface feeders and their movements likely reflect the availability of surface prey in PWS. In our study, kittiwake numbers declined after early winter, corresponding to a period when zooplankton abundance declines, diel vertical migrations of fish and euphausiids to surface waters are reduced (Cooney et al. 2001) and many forage fish species of PWS move deeper in the water column (Norcross et al. 2001). Kittiwakes were also absent in the GOA during winter surveys (Day 2006). In Europe, kittiwakes' dependence on fisheries discards increases during winter (Camphuysen et al. 1995), but there are no corresponding winter fisheries in PWS.

McKnight et al. (2011) used geolocation dataloggers to document autumn and midwinter kittiwake movements from a colony in PWS and found that birds did not remain in PWS through the winter period. Even though PWS was identified as being within the birds' wintering ranges, the authors suggest that this anomaly resulted only because a small number of birds were late in leaving the colony in October. For these tagged

birds, average distance to shore during the winter of 2007/2008 was 258 km, consistent with our lack of kittiwake observations within PWS during the same period.

Our study species' distributions range from the North Pacific (marbled murrelet) to the entire northern hemisphere (common murre and black-legged kittiwake) and the implications of our findings therefore extend beyond local relevance. The substantial temporal shifts we observed in seabird use of habitat throughout winter may also apply to other seabird species with coastal distributions during winter. In PWS, there are major seasonal shifts in species composition and abundance. For example, based on sound-wide surveys in March and July, common murre is the most numerous seabird in PWS during winter, with estimates up to 157000 birds, whereas summer estimates rarely exceed 15000 birds (McKnight et al. 2006). Thus, the PWS winter population of murres likely represents birds from multiple breeding sites, including populations outside of PWS. In contrast, the marbled murrelet is the most abundant seabird in PWS during summer, with the July estimate more than three times the estimated winter (March) population size (McKnight et al. 2006), indicating that most of the PWS breeding population winters elsewhere.

Our study illustrates that the nonbreeding season cannot be characterized as a single time period when describing seabird distribution. We found that densities of black-legged kittiwake, common murre, and marbled murrelet all varied greatly between November and March in PWS, suggesting that multiple surveys are required to quantify wintering populations and understand changes in seabird distribution. Indeed, our results also suggest that the surveys conducted across PWS in March (as in McKnight et al. 2006) have missed the winter peak in murrelet numbers, thus underestimating the importance of PWS as their midwinter habitat, when conditions are most extreme. From a conservation and management perspective, we suggest that the risk to the PWS marbled murrelet population from oil tanker and vessel accidents during midwinter is greater than

would be inferred based solely on the sound-wide March surveys.

Informed designation of protected areas or critical habitats will require better understanding of seabird habitat needs during non-breeding months. Notably, the devastating 1989 *Exxon Valdez* oil spill in PWS occurred in late March, during the seasonal transition from nonbreeding to breeding habitats for many birds, and an estimated 250000 birds were killed directly (Piatt and Ford 1996). The habitats most heavily impacted in the short and long term from this spill were protected bays with little wave action (Peterson et al. 2003)—the very habitats favored by many wintering birds, particularly small diving species like murrelets. The marbled murrelet, one of the species injured by the oil spill (Carter and Kuletz 1995, Kuletz et al. 1996), has undergone rapid population decline (Piatt et al. 2007, Kuletz et al. 2011) and, with better understanding of habitat associations, could benefit from establishment of dedicated protected areas. Effective marine spatial planning, fisheries management, and designation of marine protected areas will require improved knowledge, at a range of spatial scales, of seabird habitat selection throughout the seasons.

## Acknowledgments

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