

MARINE SPACE USE BY MARBLED MURRELETS *BRACHYRAMPHUS MARMORATUS* AT A MAINLAND FJORD SYSTEM IN SOUTHEAST ALASKA

BLAKE A. BARBAREE^{1,2}, S. KIM NELSON³ & BRUCE D. DUGGER¹

¹Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, OR 97331, USA

²Present address: Point Blue Conservation Science, 3820 Cypress Dr. #11, Petaluma, CA 94954, USA (blakebarbaree@yahoo.com)

³US Geological Survey – Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, OR 97331, USA

Submitted 24 March 2014, accepted 20 August 2014

SUMMARY

BARBAREE, B.A., NELSON, S.K. & DUGGER, B.D. 2015. Marine space use by Marbled Murrelets *Brachyramphus marmoratus* at a mainland fjord system in southeast Alaska. *Marine Ornithology* 43: 1–10.

At-sea research on Marbled Murrelets *Brachyramphus marmoratus* has been dominated by observational surveys that provide little understanding of space use by individual birds. To quantify marine space use with spatially unbiased metrics, we used radio telemetry to record nest and at-sea locations of Marbled Murrelets during the 2007 and 2008 breeding seasons at Port Snettisham in southeast Alaska. We documented considerable inter-annual variation in marine space use, indicating that foraging conditions were more favorable for Marbled Murrelets in 2007 than in 2008. Fixed kernel density estimates (FKDE) of home range size (95% FKDE) were smaller on average in 2007 ($98 \pm 10 \text{ km}^2$) than in 2008 ($158 \pm 18 \text{ km}^2$), but did not differ by sex or breeding status. Individual core use areas (50% FKDE) were not randomly distributed in our study area, and locations of population-level foraging hotspots were identified. Two large foraging hotspots were located within Port Snettisham in 2007; hotspots were less concentrated and more numerous in 2008, including small hotspots near the mouth of Tracy Arm to the south. Mean (\pm standard error) daily marine commuting distance (over the ocean) between at-sea locations and nest sites was shorter in 2007 ($12.0 \pm 0.9 \text{ km}$) than in 2008 ($20.0 \pm 2.0 \text{ km}$). Our findings suggest variable but relatively good marine habitat for Marbled Murrelets at Port Snettisham and the Holkham Bay area to the south, where Tracy Arm and Endicott Arm converge. These marine areas should be prioritized for conservation of Marbled Murrelets during the breeding season.

Keywords: seabird, space use, home range, telemetry, hotspot, Alaska, murrelet, *Brachyramphus marmoratus*

INTRODUCTION

Measurements of space use indicate how an animal responds to environmental conditions and provide information on the spatial distribution of critical resources. Seabirds typically respond to patchy and hierarchical distributions of prey by using space unevenly in the marine environment (Hunt & Schneider 1987, Russell *et al.* 1992). Seabirds are thus considered convenient indicators of marine productivity at multiple spatial and temporal scales (Cairns 1988, Croxall *et al.* 1999). Seabird home range size is a general indicator of prey availability near nesting areas because it typically displays an inverse relationship with food availability (Schoener 1983). Data on marine space use by seabirds can also reveal locations of marine hotspots (e.g., Cairns & Schneider 1990, Piatt *et al.* 2006, Suryan *et al.* 2006), help identify the oceanographic features that result in increased marine productivity (Hunt *et al.* 1998), and help define boundaries when establishing fishing zones and marine protected areas (Wilson *et al.* 2009).

During the breeding season, space use by seabirds evolves in response not only to the physical relationship between marine feeding grounds and terrestrial nest sites, but also to predation and the spatial distribution of areas with high-quality foraging conditions. In theory, breeding seabirds should minimize commute times to foraging areas by selecting nest sites in close proximity to food resources (Wittenberger & Hunt 1985, Gibbs 1991). Seabird reproductive performance may be directly linked to the

location and overall productivity of reliable foraging areas or marine hotspots (Ainley *et al.* 1995, Rindorf *et al.* 2000). Marine hotspots are defined as areas with elevated energy transfer rates between trophic levels due to relatively high primary productivity, and these areas are known to attract top predators (Sydeman *et al.* 2006). Nest sites with marine hotspots nearby should be preferred unless predation or other factors drive birds to nest farther away. In fact, studies using seabirds to identify marine hotspots have found central foraging areas with relatively high availability of foraging resources (Cairns & Schneider 1990, Piatt *et al.* 2006). Although a variety of analytical methods are available to identify marine hotspots, locating individually marked seabirds at sea is the least biased method (see review in Nelson & Boots 2008).

The Marbled Murrelet *Brachyramphus marmoratus* is a central-place foraging alcid (family Alcidae) that inhabits nearshore waters of western North America from central California to western Alaska (Nelson 1997). Marbled Murrelets (murrelets) are non-colonial and can nest up to 88 km inland from the coast (Nelson & Hamer 1995), resulting in substantial intra-specific differences in commuting costs from foraging areas to nest sites (Hull *et al.* 2001). Murrelets have also been documented flying great distances over water to reach potential foraging habitat (Whitworth *et al.* 2000, Bloxton & Raphael 2009). Estimates of the size of murrelet marine home ranges suggest considerable annual and regional variation in foraging conditions (Hébert & Golightly 2008, Bloxton & Raphael 2009). Increased marine home range sizes and commuting costs

to nest sites may affect the allocation of energy to incubation and chick provisioning (Ricklefs 1983, Eberl & Picman 1993). Thus, one might expect nesting murrelets to adopt behavioral strategies that optimize foraging efficiency and compensate for increased commuting costs, such as foraging closer to inland flyways (Peery *et al.* 2009), altering provisioning rates or payload size, or replenishing body reserves during the post-breeding period (Hull *et al.* 2001).

Around 70% of Marbled Murrelets breed in Alaska, and the highest densities during the breeding season are found in the northern portion of southeast Alaska (DeGange 1996, Piatt *et al.* 2007). However, there has never been an effort to quantify marine space use by individual murrelets in this important part of their breeding range. In this study, we used radio telemetry to collect data on murrelet marine space use at a mainland fjord system in southeast Alaska where at-sea densities of 111 murrelets per km² have been recorded (Haynes *et al.* 2011), likely because of widespread nesting habitat nearby (Raphael *et al.* 2014). We then used these data to examine murrelet home range size and marine space use patterns. First, we estimated individual home range size and tested whether home range size differed by year, sex or breeding status (Hébert & Golightly 2008). Second, we examined marine space use at the population level to determine whether distribution was clumped, indicating marine hotspots that are significant murrelet foraging habitat (Adams *et al.* 2004, Piatt *et al.* 2006). Lastly, we tested the hypothesis that murrelets nesting farther inland from the coast will mitigate commuting costs associated with increased travel over land by reducing the distance they travel over water to reach foraging areas (Hunt *et al.* 1999).

STUDY AREA AND METHODS

Our study was conducted at Port Snettisham, a remote mainland fjord located approximately 40 km south of Juneau, Alaska, United States (Fig. 1). Larger fjords are located to the north (Taku Inlet) and to the south (Tracy Arm and Endicott Arm) of Port Snettisham. Port Snettisham has three distinct sections or arms. Two arms funnel runoff from numerous river systems, including the Speel and Whiting Rivers, into a narrow, deep (up to 250 m) channel leading to Stephens Passage. The narrow but deep bathymetry of Port Snettisham creates a unique marine area with many estuarine qualities that include a large surrounding watershed, mixing of freshwater and saltwater, and opposing winds, currents and tides. Terrestrial habitat at Port Snettisham is characterized by rugged topography, little anthropogenic habitat alteration, and widespread forested and non-forested nesting habitat for Marbled Murrelets (more details in Barbaree *et al.* 2014).

Capture and radio telemetry

We used night-lighting to capture murrelets (Whitworth *et al.* 1997) near the mouth of Port Snettisham during 15–16 May 2007 ($n = 39$) and 26–28 May 2008 ($n = 40$) and tracked them from late May to early August in both years. We attached very high frequency (VHF) radio transmitters that weighed approximately 2.5 g (approximately 1% of average adult murrelet body mass) and had a lifespan of approximately 120 d to the dorsal surface of each bird using a subcutaneous anchor (Newman *et al.* 1999). We also drew a small amount of blood to determine sex. We operated under procedures and guidelines approved by the Institutional Animal Care and Use Committee of Oregon State University.

Aerial-, boat- and ground-based surveys were used to locate nest sites, monitor nest-site attendance and determine at-sea locations of radio-tagged murrelets. In both years, we used an aerial telemetry technique known as “boxing” to record the locations of radio-tagged murrelets at sea and to identify nesting areas. Boxing compares the relative signal strength received by antennas on each wing of the aircraft to determine the signal direction and to circle an area around the signal. During 2008 only, boat-based surveys were conducted in areas where murrelets were regularly detected outside the fjord during aerial surveys. As well, murrelets were surveyed by boat when convenient during marine transit for other activities. Areas regularly surveyed included the mouth of Port Snettisham, the nearshore areas between Port Snettisham and Holkham Bay, Holkham Bay, and the mouths of Tracy Arm and Endicott Arm. We used triangulation to determine the location of the radio-tagged bird if we could not pinpoint the signal to a group of murrelets. Data logger receivers were deployed at strategic locations inside Port Snettisham to record the presence and directional movements of radio-tagged murrelets throughout the fjord during the entire study (Fig. 1).

We categorized radio-tagged murrelets as either breeders or non-breeders. We defined a breeder as any bird attempting to nest at least once after capture. Nesting attempts were identified by using aerial or handheld radio-tracking to locate active nests or by using telemetry data to identify behavior patterns consistent with active incubation (Barbaree *et al.* 2014). Murrelets attend nests for 24 h shifts during incubation, resulting in an “on-off” nest attendance pattern (Nelson & Hamer 1995); thus, actively incubating birds were located at the nest site one day and at sea the following day. Based on this pattern, we defined a nest attempt as when a radio-tagged murrelet exhibited behavior indicating incubation for at least four consecutive days (on-off-on-off). We used different criteria to distinguish between active and inactive nests during the nestling-rearing period. We inferred chick provisioning flights when shore-based data loggers detected a murrelet leaving the fjord, moving towards its nest, followed by a period of no detection (range = 30–120 min) before the bird was again detected by data loggers moving through the fjord away from its nest. Based on these behavior patterns consistent with active nesting, we identified the dates that each breeder was actively attending a nest site and categorized the nesting status of at-sea locations for breeders as either active or inactive.

Home range size and foraging areas

We used fixed kernel density estimation (FKDE) to calculate the size of the marine home range of radio-tagged murrelets with at least 12 at-sea locations. We defined the marine home range (or the area an individual actually used) as the 95% portion of the utilization distribution (UD; Kernohan *et al.* 2001) and the core use area (or core foraging area) as 50% of the UD (Adams *et al.* 2004). Smoothing parameters were calculated separately for each FKDE using least-squares cross-validation (Horne & Garton 2006). We removed portions of individual UDs that covered land to estimate home range size and core use area within marine areas only.

We identified population-level central foraging areas (or foraging hotspots) by analyzing the spatial autocorrelation of individual core use areas. First, we assigned a standardized numerical value (core use area = 1; all other areas = 0) to each 30 m × 30 m cell within the FKDE data layer for each individual. Second, we merged individual

FKDEs into a single data layer with additive numerical values where core use areas overlapped. For example, if the core use areas of three birds overlapped within a single cell, the cell received a value of three. Lastly, we analyzed the resulting data layer to determine the spatial autocorrelation of the additive numerical values (using Moran's I coefficient) and to identify whether higher values were more clustered than expected by random chance (using a Getis-Ord G_i^* statistic or Z-score; Getis & Ord 1992, Ord & Getis 1995). We defined foraging hotspots as clusters of higher values with Z-scores of >1 and then further categorized hotspots as medium (Z-score 1 to 1.9) or high (>2) importance (Santora *et al.* 2010). We ran separate analyses with individuals grouped by year, sex and breeding status to visually inspect the effects of these factors on hotspot locations.

Commuting distances

The at-sea locations of breeders during active nesting (from aerial surveys only) were used to assess two factors that could influence the location of an individual at sea: year and distance of the nest site from the ocean. For each breeder, we calculated the commuting distance from each at-sea location to its nest site using straight-line distances along flight corridors (flyways) determined by watershed topography. Murrelets typically traveled over the ocean and along river corridors when commuting to their nest sites because steep topography and frequent low cloud cover prevented direct flights from marine locations to nest sites. Data from our stationary data loggers supported this assertion; for example, flight paths away from nest sites crossed an associated river mouth and led to the

mouth of Port Snettisham on at least 15 of 17 occasions when a murrelet nesting within Port Snettisham was located at sea in Tracy Arm or Holkham Bay. Commuting distances were partitioned into two components: (1) the marine commuting distance (the distance traveled over the ocean), and (2) the terrestrial commuting distance (the distance traveled over land; e.g., Fig. 2). Total commuting distance was the sum of the marine and terrestrial distances. We calculated the mean total commuting distance and mean marine distance for each breeder to reduce effects of daily variation and sample size. The terrestrial commuting distance remained constant for each breeder because it represented the distance of a nest site from the ocean. Pivot points were created to aid with straight-line distance calculations. Pivot point locations ensured that marine commuting distances did not cross land, and that terrestrial distances were measured along drainages used as flight paths to access each nest site (Fig. 2).

Statistical treatments

Our sample size of individual at-sea locations was larger in 2008 than 2007, in part because of the addition of boat-based surveys in 2008, but there was no difference in home range size in 2008 with or without boat-based detections (paired t -test; $t = 0.25$, $P = 0.80$); therefore, we included all locations in our analysis. We also used a multiple linear regression that included an interaction term (sample size \times year) to test whether the number of at-sea detections influenced the home range size of individual murrelets. Next, we used separate general linear models with home range size and core use area size as the response variables to test for effects of sex, breeding status and year. Our models included the additive effects plus two interaction

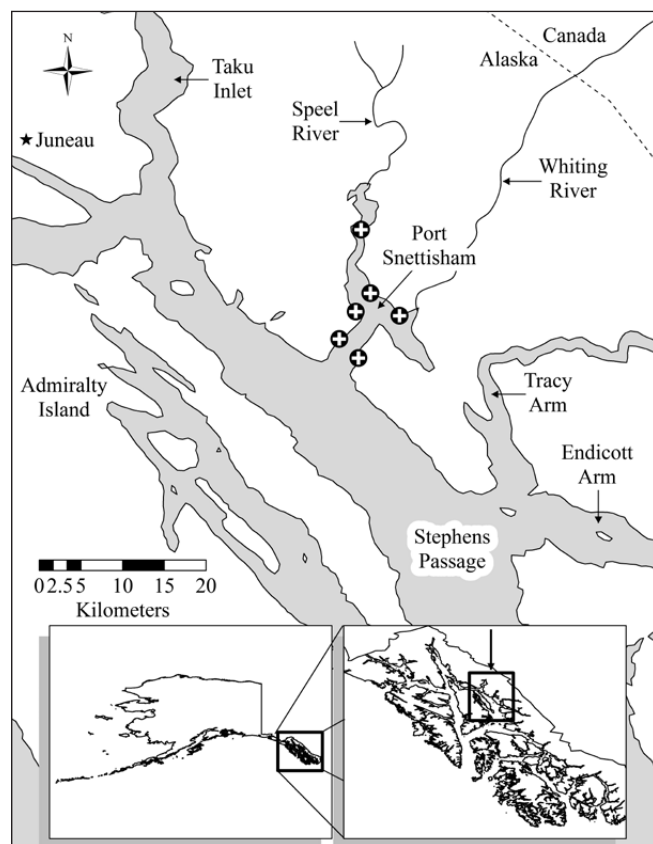


Fig. 1. Study area at Port Snettisham, southeast Alaska. Encircled white crosses indicate locations of six stationary data logger receivers that monitored presence and directional movements of radio-tagged Marbled Murrelets 24 h/day.

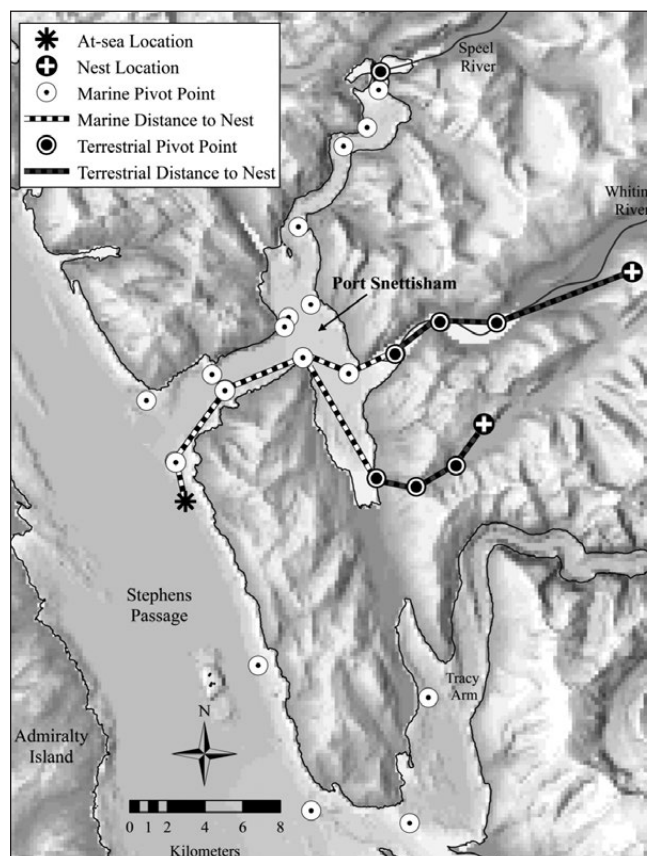


Fig. 2. Examples of measurement procedure used to estimate the distance between at-sea locations and nest sites.

terms (sex \times year + breeding status \times year) to test whether the relationship between the response variables and sex or breeding status differed between years. Two breeders in 2007 were excluded from this analysis because their sex could not be determined.

We used a multiple linear regression model to test whether mean marine commuting distance was influenced by year or terrestrial commuting distance (the distances of nest sites from the ocean).

The model included an interaction term (marine distance \times year) to test for a difference in foraging range at sea between years. Terrestrial commuting distances were not normally distributed (Shapiro-Wilk normality test; $W = 0.782$, $P < 0.0001$), so we used the natural logarithm of the raw data to achieve normality. Only breeders with at least five at-sea locations during active nesting were included in this analysis. Means are reported \pm standard deviation unless otherwise noted.

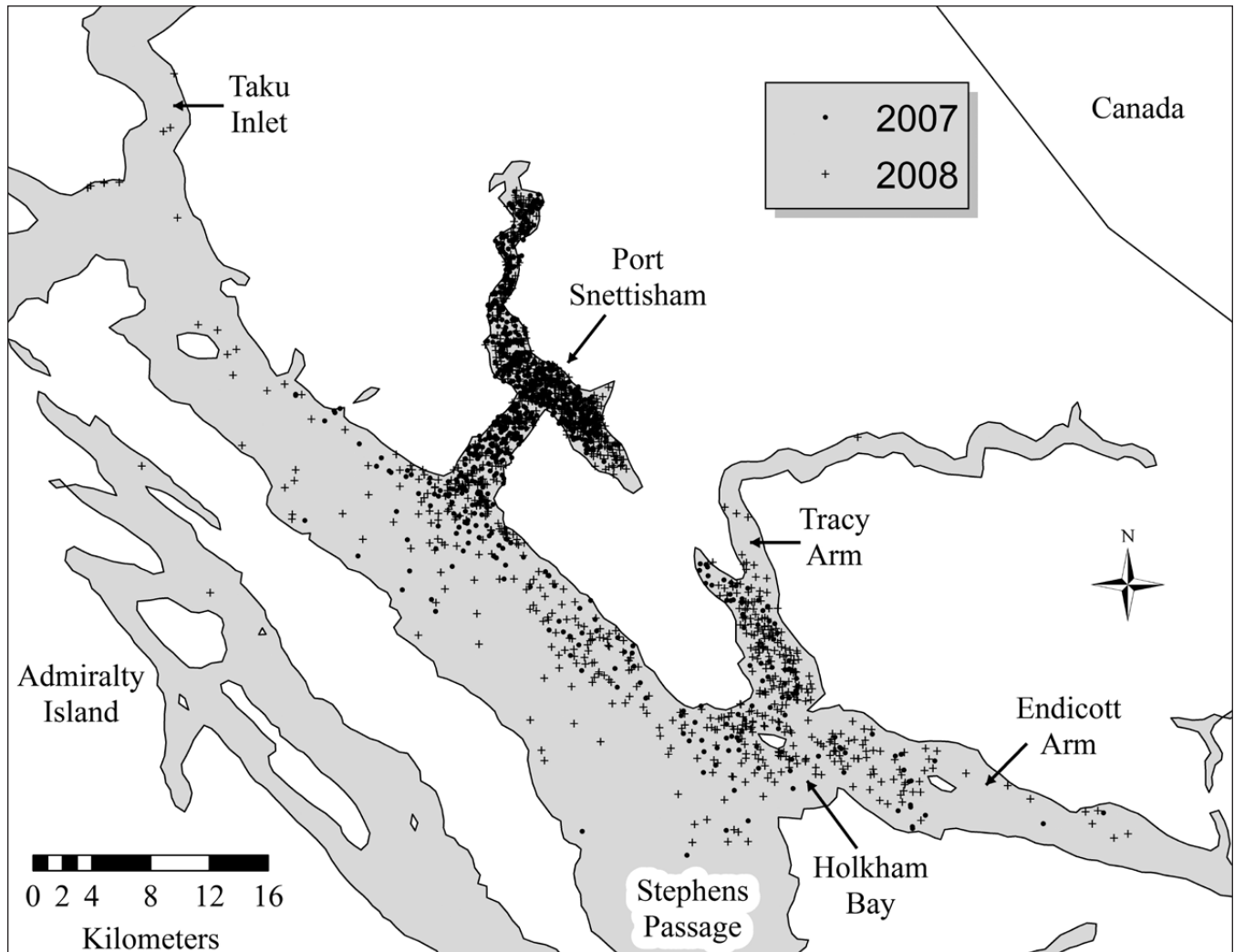


Fig. 3. At-sea locations recorded during aerial and boat-based surveys for Marbled Murrelets radio-tagged in 2007 ($n = 876$) and 2008 ($n = 1019$) at Port Snettisham, southeast Alaska.

TABLE 1
Marine home range size and mean commuting distance via flyways between at-sea locations and nest sites for radio-tagged Marbled Murrelets breeding in Port Snettisham, Alaska

Year	Mean \pm standard error							
	Home range size, ^a km ²					Commuting distances, km		
	Males	Females	Breeders	Non-breeders	All birds	Terrestrial	Marine	Total
2007	96 \pm 14 <i>n</i> = 19	107 \pm 14 <i>n</i> = 16	95 \pm 11 <i>n</i> = 21	101 \pm 18 <i>n</i> = 16	98 \pm 10 <i>n</i> = 37	15.6 \pm 3.4 <i>n</i> = 19	12.0 \pm 0.9 <i>n</i> = 19	27.7 \pm 3.4 <i>n</i> = 19
2008	168 \pm 32 <i>n</i> = 15	151 \pm 20 <i>n</i> = 20	143 \pm 21 <i>n</i> = 17	173 \pm 28 <i>n</i> = 18	158 \pm 18 <i>n</i> = 35	9.2 \pm 3.4 <i>n</i> = 10	20.0 \pm 2.0 <i>n</i> = 10	29.4 \pm 3.2 <i>n</i> = 10

^aHome range size estimated using 95% fixed kernel density estimation.

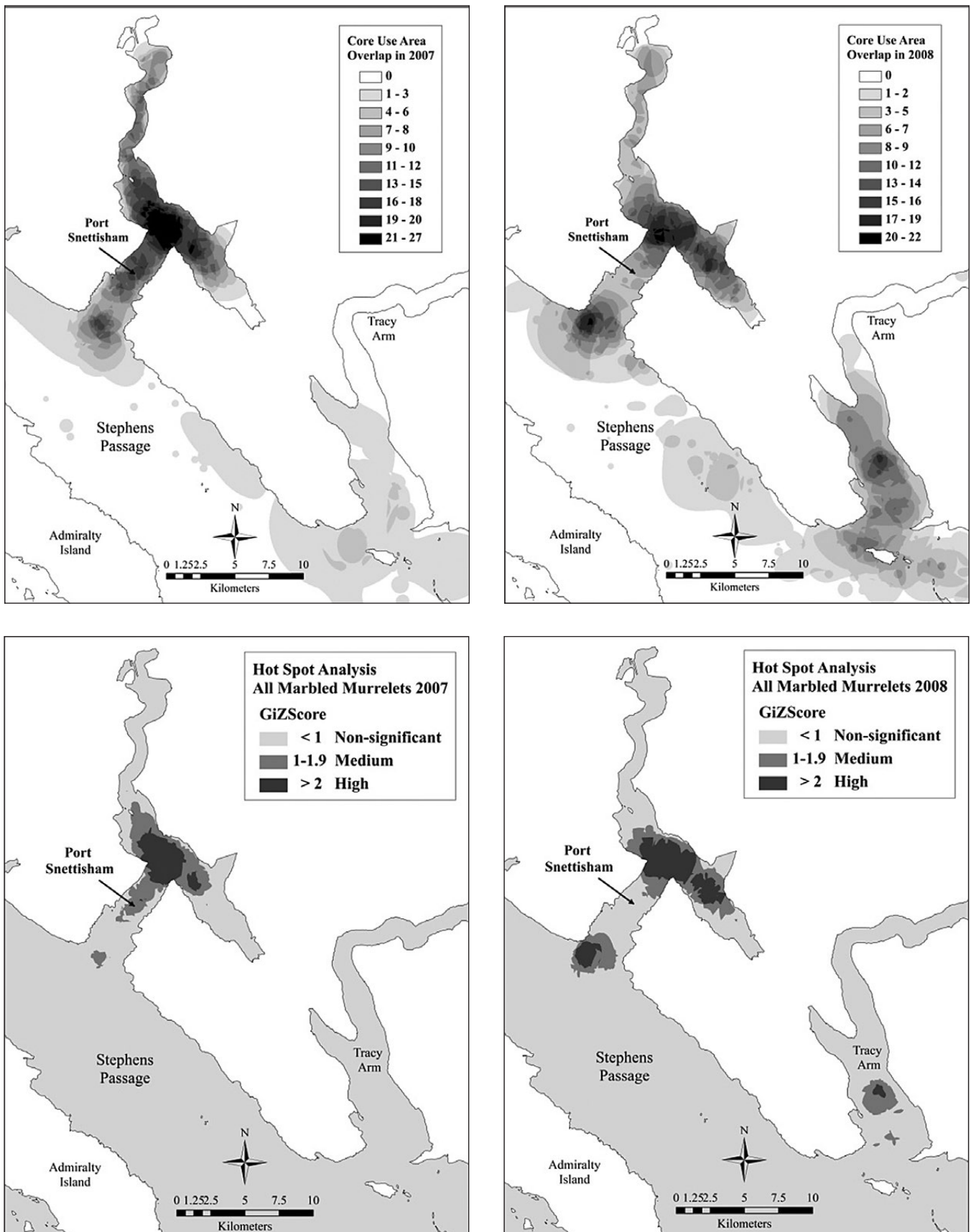


Fig. 4. Marbled Murrelet core use area overlap (top) and central-foraging hotspots (bottom) determined using the Getis-Ord G_i^* statistic and core use areas (50% fixed kernel density estimates).

RESULTS

Radio telemetry

The mean number of at-sea detections for a radio-tagged murrelet was 24.5 ± 4.4 during aerial surveys in 2007 (range 17–31, $n = 37$) and 29.7 ± 12.8 times during aerial and boat-based surveys in 2008 (range 12–55, $n = 35$). During aerial surveys, we consistently detected radio-tagged murrelets at sea within the study area when the individual was not incubating at an inland nest site and before the last detection for each individual that indicated emigration from the study area (97% of possible detections days in 2007 and 95% in 2008). Aerial and boat-based detections at sea occurred most often inside Port Snettisham, closer to the mainland in Stephens Passage, or near the convergence of Tracy Arm and Endicott Arm (Fig. 3).

Home range size and foraging areas

Mean marine home range size was 127.4 ± 88.8 km² (range 31.3–443.6 km², $n = 72$; Table 1). Mean core use area was 35.6 ± 25.6 km² (range 6.4–132.4 km², $n = 72$). The home range size of an individual murrelet was not influenced by the number of at-sea locations (all $P > 0.47$). Home range size and core use area were significantly larger in 2008 than 2007 ($F_{3,69} = 7.85$, $P = 0.007$; $F_{3,69} = 5.33$, $P = 0.024$) but did not differ by sex or breeding status (all $P > 0.27$; Table 1).

Individual core use areas were not randomly distributed. Rather, there were relatively high levels of spatial autocorrelation among core use areas in 2007 ($I = 0.22$) and 2008 ($I = 0.26$), and clusters of high core use area overlap (foraging hotspots) in 2007 and 2008 (Fig. 4). Foraging hotspots were generally smaller and less concentrated in 2008 than 2007. In 2007, at least 56% of individual core use areas overlapped in a single large foraging hotspot in central Port Snettisham, where the arms of the fjord converge. During 2008, less than 40% of individual core use areas overlapped within the same location, and additional smaller hotspots were identified near the mouth of Port Snettisham and the mouth of Tracy Arm to the south. Hotspot location did not differ according to murrelet sex. However, hotspots for breeders were located mainly within or near the mouth of Port Snettisham, while hotspots for non-breeders included areas near the mouth of Tracy Arm (Fig. 5).

Commuting distances

We recorded 342 at-sea locations during active nesting for 36 breeding murrelets, including three breeding pairs. We located 33 active nest sites, ranging from 0.1 to 52.0 km inland from the coast (terrestrial commuting distance); 29 nest sites were within the watersheds associated with Port Snettisham (see Barbaree *et al.* 2014 for more details). The mean total commuting distance (marine and terrestrial) from an at-sea location to a nest site was 28 ± 13 km ($n = 342$; range 1.5–94.2 km) and the mean marine commuting distance was 15 ± 2 km ($n = 342$; range 0.4–54.7 km). Mean marine commuting distance was shorter in 2007 than 2008 ($t = 3.32$, $P = 0.003$), but there was no difference in total commuting distances between the two years (Table 1). Terrestrial commuting distance did not influence marine commuting distance; however, there was a tendency for birds with longer terrestrial commuting distances to have shorter average marine commuting distances in 2008 but not in

2007, although the interaction term was not statistically significant ($t = -1.63$, $P = 0.115$).

DISCUSSION

Radio-tagged murrelets generally used marine habitat near the mainland and within the more protected fjords and bays where mixing of freshwater runoff and saltwater is an important oceanographic feature. When not located within Port Snettisham, murrelets typically used marine areas directly to the south. In particular, Holkham Bay and the confluence of two larger fjord systems (Tracy Arm, Endicott Arm) were heavily used, especially in 2008. The fact that more than 95% of radio-tagged murrelets, regardless of sex or breeding status, were repeatedly re-located within these areas suggests that foraging commutes to other areas were uncommon. This pattern cannot be explained solely by the need for breeders to remain near nest sites, as commuting distances to nest sites in our study area were comparatively short and even non-breeders remained in the area. Together, this suggests that foraging conditions in these mainland fjords were more optimal than in adjacent areas of Stephens Passage and other areas with less mixing of glacial and fresh waters.

A combination of factors, including oceanographic properties as well as prey abundance, quality or availability, may explain why radio-tagged murrelets foraged within these mainland fjord systems. The primary prey resource for murrelets in Port Snettisham was likely capelin *Mallotus villosus* (Haynes *et al.* 2011), a high-energy and preferred prey resource often associated with glacially affected waters (Montevecchi & Piatt 1984). Marbled Murrelets in Prince William Sound (Day *et al.* 2003) and Glacier Bay (Piatt *et al.* 2011), Alaska, preferred marine waters where glacial influence was diluted and avoided waters that were highly affected by nearby tidewater glaciers (i.e., higher turbidity, higher ice cover and lower sea surface temperature). While the marine waters in Port Snettisham and Tracy Arm are somewhat influenced by glacial runoff, which may contribute to higher capelin densities and repeated use by murrelets, this influence is limited in Port Snettisham because there are no tidewater glaciers and likely diluted around the mouth of Tracy Arm because tidewater glaciers within the fjord are located approximately 35 km away.

Mean home range size was smaller and commuting distances were shorter in 2007 than 2008, suggesting that foraging conditions within Port Snettisham were more favorable in 2007 than in 2008. Variation in freshwater runoff, which can have numerous and complex trophic-level effects in an estuarine environment (Kimmerer 2002), may help explain the difference in conditions between years. Our study coincided with a shift in the Pacific Decadal Oscillation (PDO) Index from a warm to a cold anomaly in fall 2007 (National Oceanic and Atmospheric Administration; <http://www.ncdc.noaa.gov/>). Cold-PDO anomalies have been linked to increased freshwater discharge in mainland locations of southeast Alaska (Neal *et al.* 2002), and a weather station near the mouth of the Speel River recorded more than twice as many days with rainfall ≥ 2.5 cm from June to August 2008 than the same period in 2007 (5% of days with records in 2007 vs. 11% in 2008; National Oceanic and Atmospheric Administration; <http://www.ncdc.noaa.gov/>). The bottleneck-like topography of Port Snettisham makes the fjord susceptible to rapid fluctuations in freshwater runoff. We repeatedly observed highly turbid surface water conditions prevailing throughout the fjord after high rainfall events. Murrelets

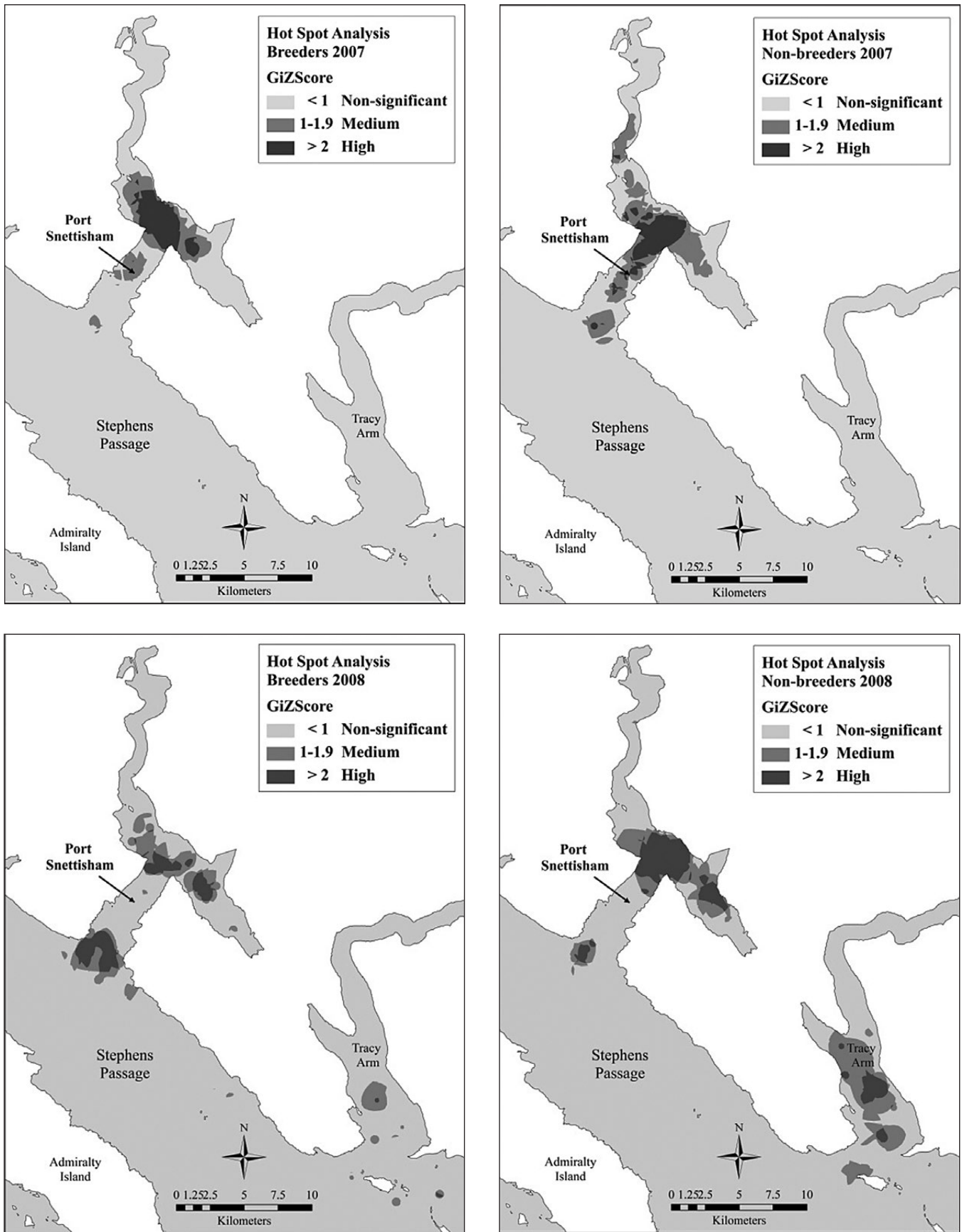


Fig. 5. Marbled Murrelet central-foraging hotspots by breeding status determined using the Getis-Ord G_i^* statistic and core use areas (50% fixed kernel density estimates).

may have avoided Port Snettisham when water conditions were highly turbid because of the drastic effect of turbidity on visual predators' ability to detect fish (Eriksson 1985) or changes in the distribution of prey.

Our estimate of mean home range size (127.4 ± 88.8 km²) was smaller than estimates from studies in northern California (505 km²; Hébert & Golightly 2008) and Washington (742 km²; Bloxton & Raphael 2009). This difference held even after we recalculated our home range estimate (154 ± 98 km²; Barbaree unpubl. data) using methods similar to those studies to make the estimates directly comparable. The differences suggest that the marine environment in and around Port Snettisham provided better foraging conditions than the California and Washington study areas (Schoener 1983). A smaller home range size also results in lower flight costs within the home range boundaries, which could result in breeding murrelets dedicating more energy to breeding activities such as incubation or chick provisioning. However, that is only true if commuting distances between nest sites and home ranges are similar, because the costs of commuting can be substantial (Hull *et al.* 2001).

A population-level analysis of overlap of home ranges identified several foraging hotspots. All hotspots were near the confluence of distinct marine systems; the large hotspot that occurred during both years was located where the three arms of Port Snettisham converge. Runoff from the entire Port Snettisham watershed converges in this section of the fjord that is less than 2 km wide but nearly 200 m deep. The confluence section of the Port Snettisham, including most of Gilbert Bay and the mouth of Speel Arm, also coincided with the highest average densities of murrelets on the water and densities of marine fish in the water column recorded during boat-based transect surveys in 2007 (Haynes *et al.* 2011). Additional hotspots in 2008 were located near the mouth of Port Snettisham and near the mouth of Tracy Arm. These hotspots appear to support similar oceanographic processes that, when combined with nesting habitat nearby (Raphael *et al.* 2014), indicate a mechanism for identifying other important foraging areas for murrelets in southeast Alaska. For example, the confluence of Icy Strait and Glacier Bay to the northwest has geography and oceanographic features similar to those of our study area, and high at-sea densities of murrelets have been recorded there during the breeding season (Piatt *et al.* 2007).

Estimates of commuting distances from at-sea locations to nest sites have varied, but those from other fjord systems are similar to our estimates. Total commuting distances via flyways to 23 nest sites at Desolation Sound, British Columbia, Canada (39 ± 23 km; Hull *et al.* 2001), and over-water commuting distances to six nest sites at Port Nellie Juan in Prince William Sound, Alaska (21 ± 6 km; Kuletz 2005), were similar to the total commuting distances (28 ± 13 km) and over-water distances in our study (15 ± 2 km). Conversely, approximately 50 km north of Port Snettisham at Auke Bay, straight-line commuting distances to nine murrelet nest sites (78 ± 27 km; Whitworth *et al.* 2000) were considerably longer than total commuting distances via flyways at Port Snettisham. Our failure to detect a tradeoff between marine and terrestrial commuting distances suggests that commuting costs for murrelets in Port Snettisham may not have represented a serious constraint to nesting murrelets, although longer marine commuting distances in 2008 suggested that breeders extended their foraging range farther than in 2007.

Results from our study suggest that Port Snettisham and nearby marine areas to the south are important foraging habitat for murrelets during the breeding season and that all marine habitats should not be viewed as equal. The marine hotspots that we documented should be identified as priority areas for conservation during the breeding season. Investigating potential relationships between foraging hotspots and human activities, such as commercial fishing, within and near Port Snettisham might help improve our understanding of how human activities and murrelets habitat needs intersect. More generally, if hotspots are a common feature of marine space use by murrelets in southeast Alaska, a better understanding of features that create them could help improve surveys designed to estimate murrelet population size and trends.

ACKNOWLEDGEMENTS

Field research was funded by the Alaska Department of Fish and Game (ADFG), Division of Wildlife Conservation, through a cooperative agreement with the EcoHealth Alliance (formerly Wildlife Trust, Inc.) and Oregon State University. Additional funding was provided by the Department of Fisheries and Wildlife at Oregon State University and the US Geological Survey through the Oregon Cooperative Wildlife Research Unit. Thanks to M. Rabe (ADFG) for facilitating this research. We especially thank S. Newman, D. Whitworth, and H. Carter for facilitating and assisting this work. We also thank M. Kirchhoff (formerly of ADFG) who encouraged us to conduct a radio-telemetry project on Marbled Murrelets at Port Snettisham and provided extensive assistance, field equipment and fundamental advice. M. Loverink, owner and chief pilot of Air Excursions in Juneau, Alaska, provided transportation and high-quality aerial-telemetry flights. Field support was provided by excellent field and capture crew members G. Brooks, D. Cushing, T. Haynes, V. Padula, S. Plumb, S. Thomsen, and numerous volunteers including G. Baluss, R. Barbaree, A. Deutschlander, P. Hébert, R. Kinsella, M. Kissling, S. McAllister, M. Mauntler, S. Moore, Z. Peery, M. Rabe, K. Savage, G. Van Vliet and L. Watts. The comments of A. Burger and M. Rodway greatly improved the paper.

REFERENCES

- ADAMS, J., TAKEKAWA, J.Y. & CARTER, H.R. 2004. Foraging distance and home range of Cassin's Auklets nesting at two colonies in the California Channel Islands. *Condor* 106: 618–637.
- AINLEY, D.G., SYDEMAN, W.J. & NORTON, J. 1995. Upper trophic level predators indicate interannual negative and positive anomalies in the California Current food web. *Marine Ecology Progress Series* 118: 69–79.
- BARBAREE, B.A., NELSON, S.K., DUGGER, B.D., ROBY, D.D., CARTER, H.R., WHITWORTH, D.L. & NEWMAN, S.H. 2014. Nesting ecology of Marbled Murrelets at a remote mainland fjord in southeast Alaska. *Condor: Ornithological Applications* 116: 173–184.
- BLOXTON, T.D. & RAPHAEL, M.G. 2009. Breeding ecology of the Marbled Murrelet in Washington State: 5-year project summary. Olympia, WA: USDA Forest Service, Pacific Northwest Research Station.
- CAIRNS, D.K. 1988. Seabirds as indicators of marine food supplies. *Biological Oceanography* 5: 261–271.
- CAIRNS, D.K. & SCHNEIDER, D.C. 1990. Hot spots in cold water: feeding habitat selection by Thick-billed Murres. *Studies in Avian Biology* 14: 52–60.

- CROXALL, J.P., REID, K. & PRINCE, P.A. 1999. Diet, provisioning and productivity responses of marine predators to differences in availability of Antarctic krill. *Marine Ecology Progress Series* 177: 115–131.
- 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.
- DEGANGE, A.R. 1996. A conservation assessment for the Marbled Murrelet in Southeast Alaska. Gen. Tech. Rep. PNW-GTR-388. Portland, OR: USDA Forest Service.
- EBERLE, C. & PICMAN, J. 1993. Effect of nest-site location on reproductive success in Red-throated Loons (*Gavia stellata*). *Auk* 110: 436–444.
- ERIKSSON, M.O.G. 1985. Prey detectability for fish-eating birds in relation to fish density and water transparency. *Ornis Scandinavica* 16: 1–7.
- GETIS, A. & ORD, K. 1992. The analysis of spatial association by use of distance statistics. *Geographical Analysis* 24: 189–206.
- GIBBS, J.P. 1991. Spatial relationships between nesting colonies and foraging areas of Great Blue Herons. *Auk* 108: 764–770.
- HAYNES, T.B., NELSON, S.K., POULSON, F. & PADULA, V.M. 2011. At-sea habitat use and patterns in spatial distribution of Marbled Murrelets in Port Snettisham, southeast Alaska. *Marine Ornithology* 39: 151–162.
- HÉBERT, P.N. & GOLIGHTLY, R.T. 2008. At-sea distribution and movements of nesting and non-nesting Marbled Murrelets (*Brachyramphus marmoratus*) in northern California. *Marine Ornithology* 36: 99–105.
- HORNE, J.S. & GARTON, E.O. 2006. Likelihood cross-validation versus least squares cross-validation for choosing the smoothing parameter in kernel home-range analysis. *Journal of Wildlife Management* 70: 641–648.
- HULL, C.L., KAISER, G.W., LOUGHEED, C., LOUGHEED, L., BOYD, S. & COOKE, F. 2001. Intraspecific variation in commuting distance of Marbled Murrelets (*Brachyramphus marmoratus*): ecological and energetic consequences of nesting further inland. *Auk* 118: 1036–1046.
- HUNT, G.L., RUSSELL, R.W., COYLE, K.O. & WEINGARTNER, T. 1998. Comparative foraging ecology of planktivorous auklets in relation to ocean physics and prey availability. *Marine Ecology Progress Series* 167: 241–259.
- HUNT, G.L. & SCHNEIDER, D.C. 1987. Scale-dependent processes in the physical and biological environment of marine birds. In: Croxall, J.P. (Ed.) *Seabirds: feeding ecology and role in marine ecosystems*. Cambridge, UK: Cambridge University Press. pp. 7–41.
- HUNT, G.L., MEHLUM, F., RUSSELL, R.W., IRONS, D., DECKER, M.B. & BECKER, P.H. 1999. Physical processes, prey abundance, and the foraging ecology of seabirds. In: Adams, N.J. & Slotow, R.H. (Eds.) *Proceedings of the 22nd International Ornithological Congress*, Durban, South Africa. Johannesburg, South Africa: Birdlife South Africa. pp. 2040–2056.
- KERNOHAN, B.J., GITZEN, R.A. & MILLSPAUGH, J.J. 2001. Analysis of animal space use and movements. In: Millspaugh, J.J. & Marzluff, J.M. (Eds.) *Radio tracking and animal populations*. San Diego, CA: Academic Press. pp. 126–166.
- KIMMERER, W.J. 2002. Effects of freshwater flow on abundance of estuarine organisms: physical effects or trophic linkages? *Marine Ecology Progress Series* 243: 39–55.
- KULETZ, K.J. 2005. Foraging behavior and productivity of a non-colonial seabird, the Marbled Murrelet (*Brachyramphus marmoratus*), relative to prey and habitat. Ph.D. dissertation. Victoria, BC: University of Victoria.
- MONTEVECCHI, W.A. & PIATT, J. 1984. Composition and energy contents of mature inshore spawning Capelin (*Mallotus villosus*): implications for seabird predators. *Journal of Comparative Biochemistry and Physiology* 78A: 15–20.
- NEAL, E.G., WALTER, M.T. & COFFEEN, C. 2002. Linking the Pacific decadal oscillation to seasonal stream discharge patterns in Southeast Alaska. *Journal of Hydrology* 263: 188–197.
- NELSON, S.K. 1997. Marbled Murrelet (*Brachyramphus marmoratus*). In: Poole, A. & Gill, F. (Eds.) *Birds of North America*, No. 276. Philadelphia, PA, and Washington, DC: The Academy of Natural Sciences and The American Ornithologists Union.
- NELSON, S.K. & HAMER, T.E. 1995. Nesting biology and behavior of the Marbled Murrelet. In: Ralph, C.J., Hunt, Jr., G.L., Raphael, M.G. & Piatt, J.F. (Eds.) *Ecology and conservation of the Marbled Murrelet*. Gen. Tech. Rep. PSW-GTR-152. Albany, CA: USDA Forest Service. pp. 57–67.
- NELSON, T.A. & BOOTS, B. 2008. Detecting spatial hot spots in landscape ecology. *Ecography* 31: 556–566.
- ORD, J.K. & GETIS, A. 1995. Local spatial autocorrelation statistics: distributional issues and an application. *Geographic Analysis* 27: 286–306.
- PEERY, M.Z., NEWMAN, S.H., STORLAZZI, C.D. & BEISSINGER, S.R. 2009. Meeting reproductive demands in a dynamic upwelling system: foraging strategies of a pursuit diving seabird, the Marbled Murrelet. *Condor* 111: 120–134.
- PIATT, J.F., WETZEL, J., BELL, K., DEGANGE, A.R., BALOGH, G.R., DREWA, G.S., GEERNAERTE, T., LADD, C. & BYRD, G.V. 2006. Predictable hotspots and foraging habitat of the endangered Short-tailed Albatross (*Phoebastria albatrus*) in the North Pacific: Implications for conservation. *Deep-Sea Research II* 53: 387–398.
- 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. Open-File Report 2006–1387. US Geological Survey.
- RAPHAEL, M.G., SHIRK, A.J., FALXA, G.A. & PEARSON, S.F. 2014. Habitat associations of Marbled Murrelets during the nesting season in nearshore waters along the Washington to California coast. *Journal of Marine Systems* <http://dx.doi.org/10.1016/j.jmarsys.2014.06.010>.
- RICKLEFS, R.E. 1983. Avian postnatal development. In: Farner, D.S., King, J.R. & Parkes, K.C. (Eds.) *Avian biology*, vol. 7. New York: Academic Press. pp. 2–88.
- RINDORF, A., WANLESS, S. & HARRIS, M.P. 2000. Effects of changes in sandeel availability on the reproductive performance of seabirds. *Marine Ecology Progress Series* 202: 241–252.
- RUSSELL, R.W., HUNT JR., J.L., COYLE, K.O. & COONEY, R.T. 1992. Foraging in a fractal environment: Spatial patterns in a marine predator-prey system. *Landscape Ecology* 7: 195–209.
- SANTORA, J.A., REISS, C.S., LOEB, V.J. & VIET, R.R. 2010. Spatial association between hotspots of Baleen Whales and demographic patterns of Antarctic krill *Euphausia superba* suggests size-dependent predation. *Marine Ecology Progress Series* 405: 255–269.
- SCHOENER, T.W. 1983. Simple models of optimal feeding-territory size: reconciliation. *American Naturalist* 121: 608–629.
- SURYAN, R.M., SATO, F., BALOGH, G.R., HYRENBACH, K.D., SIEVERT, P.R. & OZAKI, K. 2006. Foraging destinations and marine habitat use of Short-tailed Albatrosses: A multi-scale approach using first-time passage analysis. *Deep-Sea Research II* 53: 370–386.

- SYDEMAN, W.J., BRODEUR, R.D., GRIMES, C.B., BYCHKOV, A.S. & MCKINNELL, S. 2006. Marine habitat "hotspots" and their use by migratory species and top predators in the North Pacific Ocean: Introduction. *Deep-Sea Research Part II* 53: 247–249.
- WHITWORTH, D.L., TAKEKAWA, J.Y., CARTER, H.R. & MCIVER, W.R. 1997. Night-lighting as an at sea capture technique for Xantus' Murrelets in the southern California Bight. *Colonial Waterbirds* 20: 525–531.
- WHITWORTH, D.L., NELSON, S.K., NEWMAN, S.H., VAN VLIET, G.B. & SMITH, W.P. 2000. Foraging distances of radio-marked Marbled Murrelets from inland areas in Southeast Alaska. *Condor* 102: 452–456.
- WILSON, L.J., MCSORLEY, C.A., GRAY, C.M., DEAN, B.D., DUNN, T.E., WEBB, A. & REID, J.B. 2009. Radiotelemetry as a tool to define protected areas for seabirds in the marine environment. *Biological Conservation* 142: 1808–1817.
- WITTENBERGER, J.F. & HUNT, G.L. 1985. The adaptive significance of coloniality in birds. In: Farner, D.S., King, J.R. & Parkes, R.C. (Eds.) *Avian biology*, Vol. 8. New York: Academic Press. pp. 1–78.
-