At-sea Habitat Use and Patterns in Spatial Distribution of Marbled Murrelets in Port Snettisham, SE Alaska

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ABSTRACT

We examined prey availability, habitat use, and spatial distribution of Marbled Murrelets (*Brachyramphus marmoratus*) during summer 2007 in Port Snettisham (PS), AK. Strip transects revealed that Marbled Murrelets were the dominant seabird species found on the water within our study area (93 % of all surveyed birds). We sampled murrelet prey using beach seining, plankton tows, and dip-netting, and found that capelin (*Mallotus villosus*), Pacific sand lance (*Ammodytes hexapterus*), and other preferred forage fish species occurred in PS. All mixed forage flocks of birds had murrelets present and capelin were the only prey item found in dipnet samples from forage flocks within PS. The presence of adult, young of the year, and larval capelin suggested that PS was used by capelin as spawning habitat and capelin were likely the primary prey item in the area for murrelets. We found that murrelets moved to more exposed, deeper waters, more distant from the shore at night compared to during the day where they were found in PS, and this difference was not related to differing prey abundances. We modeled murrelet distribution at fine (100, 200, 400, 800, and 1600 m) and meso (14.4 km) scales using classification and regression tree (CART) analysis. At fine-scales, we examined murrelet density, number of groups, and presence-absence based on distance to creek, distance to shoreline, distance to flyway, mean depth, tidal slick count, prey schools$\cdot$km^{-1}, prey relative abundance$\cdot$km^{-1}, and tidal stage. At almost all fine scales, distance to flyways was the most important variable with prey variables becoming more important as scale increased. However, CART models of fine-scale habitat use did not perform well (*e.g.*, at the 100 m scale the regression tree only explained 9.8% of the variance). At the meso-scale, we examined murrelet abundance and number of groups based on breeding period, tidal stage, time of day, prey schools$\cdot$km^{-1}, prey relative abundance$\cdot$km^{-1}, and tidal slick count. We found that low prey availability was associated with lower abundances of murrelets. However, we found that during low prey availability murrelets were more abundant during nest incubation and chick rearing compared with nest initiation and post-breeding, suggesting that murrelets remain close to nesting habitat during periods when inland flights are frequent. Models at meso-scale performed well explaining almost 50% of the variation. We used Ripley's K to examine spatial clustering by murrelets relative to each other (univariate) and their prey (bivariate). Murrelets showed significant spatial clustering relative to one another on all transects with a patch length (scale of clustering) ranging from 0.3 to 9.0 km. Patch length increased significantly at the end of the breeding season (during chick rearing/post breeding). For 18 of the 20 sample days, murrelets were significantly clustered with prey, however, the scale of clustering showed high variation. Despite the high variation, murrelets tracked prey down to the finest scale of analysis (100 m) on 8 of the 18 days suggesting a generally high concordance. On days where murrelet mean group size was relatively high (>2.33 murrelets$\cdot$group^{-1}), murrelets tracked prey at a significantly finer scale and had significantly lower patch lengths suggesting that larger groups are more closely associated with fish and closer to other groups of murrelets. Comparing clustering characteristics among three different prey abundance categories (low, medium, high), we found murrelets tracked prey over a broader range of scales at medium relative prey abundances. Overall, these results add to the body of knowledge regarding how murrelets use marine habitat during breeding season.

Results provide information about temporal and spatial distributions of murrelets as well as prey occurrence in an area where breeding numbers are likely high relative to other regions across their range.

INTRODUCTION

The distribution of seabirds within the marine environment is strongly influenced by space and time. The environmental and social factors that influence seabird distributions are dependent on scale (Hunt and Schneider 1987, Swartzman and Hunt 2000), with seabirds likely making spatially hierarchical decisions in selecting habitat (Fauchald *et al.* 2000, Becker and Beissinger 2003). One of the major influences on seabird distributions is the distribution and availability of prey (Tasker *et al.* 1985). Although seabirds are expected to show a strong aggregative response to their prey, this is often not the case, especially at small scales (Woodby 1984, O'Driscoll 1998, Swartzman and Hunt 2000, Fauchald and Erikstad 2002). At larger scales, seabirds occupy the same general regions as their prey (*e.g.,* Logerwell and Hargreaves 1996). As the scale becomes finer, the spatial associations between seabirds and prey become weak or highly variable (Fauchald and Erikstad 2002) and are dependent on prey patch size (Davoren 2000) and prey abundance (Vlietstra 2005). Other factors play a role in determining the relationship between seabirds and their prey including: energetics (*e.g.,* molting; Davoren *et al.* 2002), competition (*e.g.,* Burger *et al.* 2008, Ronconi 2008), and prey behavior (Woodby 1984, Logerwell and Hargreaves 1996, Zamon 2003).

The Marbled Murrelet (*Brachyramphus marmoratus*, hereafter murrelet) is a small alcid whose biology has received much attention due to their conservation status (USFWS 1992, McShane *et al*. 2004). From 2004 – 2006, the total North American census size was estimated to be 300,000 – 400,000 individuals, with roughly 80% of the birds occurring in Alaska (Piatt *et al*. 2006). In 2008, the United States Fish and Wildlife Service (USFWS) chose to review the protected status of this species, with a complete review of its population status and biology throughout its range (Zelkowitz 2008). Because murrelets spend the majority of their lives at sea, the marine ecology of the murrelet has particularly important implications for its conservation and management.

The marine distribution of murrelets has been studied on coast-wide (*e.g.,* Yen *et al*. 2004), regional (*e.g.,* Ostrand *et al.* 1998, Becker and Beissinger 2003, Day *et al.* 2003, Ronconi 2008), and local scales (*e.g.,* Becker and Beissinger 2003, Ronconi 2008). Researchers have found close associations between marine conditions and the reproductive success and population trends of murrelets (Becker *et al.* 2007, Norris *et al.* 2007, Piatt *et al*. 2007). Although the marine ecology of the murrelet has been examined over the past two decades, only recently have researchers begun to examine their marine habitat requirements (Ronconi 2008). As knowledge of their marine habitat requirements grows, researchers will be better able to understand the biology of this species, and incorporate this information into conservation and management decisions.

Murrelets are unique in that they are the only known alcid species to nest in old-growth forests (Nelson 1997). Additionally, the marine distributions of murrelets are markedly different from other piscivorous alcids on the southwest coast of Vancouver Island, British Columbia (Burger *et al*. 2008). In parts of Alaska, murrelet populations have been correlated with schools of prey (Ostrand *et al*. 1998). However, little is known about the marine habitat distribution and marine habitat requirements of murrelets in southeast Alaska, the geographic center of their range (Piatt *et al*. 2007). With their protected status under review by USFWS, it is critical to gather information on the marine habitat use of this species throughout their entire range.

In this study, we examined four aspects of the spatial distribution and habitat use of murrelets at-sea. First, we used a multiscale approach to examine fine-scale (0.1 – 1.6 km) distribution in relation to local habitat characteristics and prey distribution. Second, we used a 14.3 km section of transect to determine the effects of habitat characteristics as well as breeding period, tidal cycle, and time of day on murrelet habitat use. Third, we examined the effects of the diel cycle on murrelet distribution by comparing night and day survey values for different areas within our study region. And fourth, we used Ripley's K statistic (Ripley 1981), a measure of spatial clustering, to examine whether murrelets were clustered relative to one another and relative to prey. We expect that prey abundance and distribution will play an important role in the at-sea distribution of murrelets in southeast Alaska during their breeding season, although other factors likely influence their distribution as well.

METHODS

Study Area

Port Snettisham (PS) is located about 40 km south of Juneau in Southeast Alaska (Figure 1). It is part of a large system of channels with fjord characteristics, has a water surface area of about 80 km^2, is surrounded by intact old-growth forest and is relatively undeveloped except for a few small cabins, and a power station and fish hatchery located in the northeastern end of Speel Arm. PS's oceanography is strongly influenced by freshwater inputs from two major watersheds, the Speel and the Whiting Rivers, along with numerous perennial creeks. Strong tidal action mixes this freshwater with saltwater draining into Steven's Passage to the southeast. PS is located 150 km from the open ocean and is protected from oceanic circulation patterns by Admiralty and Chichagof islands.

Murrelet at-sea sampling

Murrelet survey transects zigzagged from shoreline to shoreline and were oriented based on visible shoreline landmarks that aided in navigation (Figure 1). We conducted surveys May – July 2007 in seas with a Beaufort sea state ≤ 3 and visibility across the water > 50 m. We sampled seabirds using a 100-m-wide fixed width strip transect in a 6.1 m aluminum hull vessel traveling at 14 $km \cdot h^{-1}$. Two observers, one on each side of the bow (eye elevation about 2.5 m) used digital voice recorders to record the observation time and the number of birds sitting on the water along a 50 m line on either side of the boat (total 100 m width) that ran perpendicular (abeam) to the vessel. When birds flushed off the water due to the presence of the survey vessel, observers noted their last location on the water and recorded the time when that location passed perpendicular to and within 50 m of the vessel. Periodically, we towed a buoy 50 m behind the vessel in order to aid the observers in estimating the strip width. Birds within 2 m of each other were recorded as being in a group (Becker *et al.* 1997). Birds in flight were not considered.

Observers noted the time the research vessel crossed a tidal disturbance (hereby referred to as "tidal slicks"). Tidal currents can create physical structure in the water column that can be detected at the surface (Thomson 1981). For example, tidal disturbances can cause upwelling which is visible at the surface as smooth linear disturbances or downwelling which is visible at the surface as linear collections of debris (Holm and Burger 2002). Prey and foraging activity of diving seabirds have been associated with tidal structure (Decker and Hunt 1996, Holm and Burger 2002, Zamon 2003).

A third observer monitored a 200 kHz echosounder (Furuno FCV 585). The sounder screen was overlaid with a grid (5mm x 5mm grid size) and the depth scale was set to 0 – 60 m. For each target seen on the echosounder, the observer recorded the time the target appeared, target depth, bottom depth, target size (based on grid) and strength. Strength of the target was scored as either strong (targets that showed at least a portion of the signal as the highest intensity) or weak (all other targets). Because we had a high number of weak targets that appeared to be due to halocline signal or other "noise", we only considered targets that were categorized as "strong" for analysis. When examining relationships between prey and murrelet distributions, target signals below 40 m were removed because beyond this depth prey would generally be inaccessible to diving murrelets (Burger *et al.* 2004).

A GPS (Garmin 76cs) recorded time-stamped track points every 10 s during the survey. After the survey, birds, tidal slicks, and echosounder targets recorded by the observers were given a waypoint by associating the time of each observation with the track point closest in time.

Daytime surveys were collected over the entire study area (T1-T16, Figure 1) seven times through the season on a biweekly basis. We surveyed the section T6-T9 an additional 18 times (total of 25 T6-T9 surveys including the times surveyed with T1-T16). T6-T9 was sampled more frequently to provide a larger sample size so we could test the effects of the tidal cycle, time of day (TOD), and breeding period on the murrelet distribution. Low and high tide periods were classified as the 1 h period before and after the low or high tide. TOD was categorized as follows: (1) dawn (03:00:00-06:00:00 h); (2) morning (06:00:01-12:00:00 h); (3) afternoon (12:00:01-19:00:00 h); and (4) dusk (19:00:01-22:00:00 h). Based on telemetry observations collected within our study region by a concurrent study examining nesting habitat (Nelson *et al.* 2008), we categorized the breeding season into three periods: (1) nesting initiation (25-May to 18-June); (2) incubation (19-June to 12-July); and (3) chick rearing and post breeding (13 to 27-July).

We conducted night surveys in two regions: T15-T16 and T6-T9 (Figure 1), six times in each region in both day and night hours. T15-T16 is exposed to the weather conditions of Steven's Passage and further from shorelines compared to T6-T9 within the protected waters of PS. Night surveys required the use of spotlights (1.5 million candlepower) fixed with aluminum tubing to focus the beam. Two observers, one on each side of the bow, scanned continuously using a 90^{o} arc beginning in the direction of travel to perpendicular to the direction of travel (*i.e.,* abeam off the port or starboard) and back. Birds were counted within a 50 m strip on either side of the vessel. We calibrated the 50 m distance estimate using the same buoy towed behind the boat as in the day. Bird and sounder observations were recorded in the same manner as during day surveys.

Prey Sampling

We used three sampling methods to document possible murrelet prey items in PS: (1) dip-netting, (2) beach seining, and (3) plankton towing. We collected dip-net samples of prey opportunistically from May 22-July 18 (N = 18) at foraging flocks with murrelets present. We beach seined at 14 different sites with three of the sites sampled twice. For the first portion of the season we used a beach seine that was 30.5 x 1.8 m with a mesh size of 9.5 mm. From 14-July on, we used a smaller meshed beach seine with a knotless 4 mm stretch mesh net, 9.2 m in length with a 3.1 m centre that tapered to 1.1 m at the wings. We conducted two beach seine replicates at each site at low tide because this is generally the most effective time to sample nearshore fishes (Haynes 2006). We conducted plankton tows in July 2007 at T14-T16 and T6-T9. Four sample points were placed at random along each transect section no closer than 500 m to each other. At each station, a small rectangular plankton net (45 cm x 25 cm, 500 micron mesh) was dropped to 50 m and towed obliquely for 5 minutes. T6-T9 was sampled twice and T15-T16 was sampled three times. Due to logistics of sampling at night during the summer when the time between sunset and sunrise is short, we were able to sample plankton for T6-T9 and T15-T16 during the same night only once.

Statistical analysis

Fine-scale habitat use

We examined murrelet distribution along one transect length (T1-T16, Figure 1) at five linear lengths or scale “grains”: 100, 200, 400, 800, 1600 m. Murrelet density (murrelets$\cdot$km^{-2}), group count (groups$\cdot$km^{-2}), and presence-absence as well as eight independent habitat variables were summarized for each bin at each scale. All spatial data manipulation and extractions were done in ArcGIS 9.2 (ESRI).

Murrelet density and group count were analyzed in relation to: distance to creek, distance to shoreline, distance to flyway, mean depth, tidal slick count, prey schools (schools$\cdot$km^{-1}), prey relative abundance (pixels$\cdot$km^{-1}) and tidal stage. Distance to nearest creek, shoreline and major flyway were taken as the linear distance from the bin centroid to the feature. There were three important flyways for murrelets traveling inland to nesting habitat: Speel River, Whiting River, and Gilbert Bay (Nelson *et al*. 2008, Figure 1). We calculated distance of each bin to the closest flyway. Depth for the transect was calculated from sounder data taken over the season and interpolated using Inverse Distance Weighting (IDW). Mean depth was the average depth for the bin area. Tidal slick count is the number of visible disturbances in the water surface created by currents or tidal upwelling recorded in each bin. Prey schools·km^{-1} was the number of targets seen on the echosounder per km while prey relative abundance·km^{-1} was the sum of the target pixels (based on the grid over the display screen) per km. Tidal stage for the bin was categorized as the stage (rising, high, falling or low, as described above) at the time the bin was surveyed.

Univariate analysis – We explored univariate relationships between continuous variable pairs at the 100 m bin scale by examining Spearman's correlation coefficients (r_s) and the relationship between murrelet presence-absence and the independent variables using Mann-Whitney U tests.

CART analysis – We analyzed murrelet distribution with respect to environmental characteristics using Classification And Regression Tree (CART) methods. CART uses constraints rather than correlates to analyze data (O'Connor 2002), which is more realistic in for habitat selection or use models (Huston 2002). Thus, CART models are likely to be more robust compared with traditional techniques that rely on linear correlations such as Generalized Linear Models (GLM's). Also, CART deals automatically with non-parametric data, interaction effects, non-linear predictors, and spatial autocorrelation. These concerns can confound GLM's by causing a violation of assumptions (O'Connor 2002, Muñoz and Felicísimo 2004). All CART associated statistical analyses were conducted in SPSS (Version 15.0).

We ran preliminary CART analyses to determine the importance of each dependent variable in relation to murrelet distribution at the five scales for each dependent variable: murrelet presence-absence, density, and group count. At each spatial scale, ten trees were grown for each dependent variable. Bins were not averaged across dates for analysis. Each tree subsampled about 250 points randomly from each dataset. Bivariate CART analysis can be affected by the presence-absence ratio (*i.e.*, high proportions of absence counts, De'ath and Fabricius 2000). To compensate for deviations in the 50:50 presence to absence ratio for each bin size we used a weighted influence variable to account for differences in the presence to absence ratio (Ronconi 2008). Trees were grown using the Gini impurity measure with a liberal minimum improvement of 0.00001 and no pruning to induce growth, a maximum tree depth of five, and a minimum of ten cases in a parent node and five cases in the child node for growth to continue.

Importance values for independent variables were calculated as the weighted sum across all tree nodes of the improvements that an independent variable has when it is used as a primary or surrogate splitter (Breiman *et al.* 1984).

We built one final tree at the 100 m bin size for each dependent variable using bin values averaged across dates for each variable (*i.e.*, each bin has only one value for each variable based on average values from the seven surveys). Averaging bins temporally decreases the sample size but helps maintain spatial independence of points. The tidal stage variable was not included because its values could not be averaged. We designated murrelets as present if they were present in the bin more times than the mean number of times they were present in all bins for that scale and absent if they were present less times than the mean. Trees were built using the same methods as above but were pruned using the 1-standard deviation rule (Breiman *et al.* 1984). We used 80% of the data to build the trees (training set) and cross-validated using the remaining 20% (test set).

Meso-scale habitat use

We used a 14.4 km section of the transect (T6-T9, Figure 1) to test the relationship for both murrelet density and group count with breeding period, tidal stage, time of day, prey schools, prey relative abundance, and tidal slick count. This section was sampled 25 times throughout the season and was treated as the scale grain for the mesoscale analysis.

Univariate analysis – We examined Spearman's correlation coefficients (r_s) between continuous variables. We compared murrelet density among breeding periods, TOD, and tidal stage using Kruskal-Wallis tests. In addition to the four TOD categories we also collapsed categories into: (1) dawn-morning (03:00:00-12:00:00 h) and (2) afternoon-dusk (12:00:01-22:00:00 h), and compared murrelet density, group count, prey schools, and prey relative abundance between these two time periods using the Mann-Whitney U test statistic. Similarly, for tidal stage we compared murrelet density in relation to four stages: low, rising, high and falling (described above) and the collapsed categories: (1) slack (low and high tide periods), and (2) rise-fall (rising and falling tide periods) using a Mann-Whitney U test.

CART analysis – We ran a regression tree analysis for each of the two continuous dependent variables (murrelet density and group count) at the scale of the T6-T9 transect (N = 25). The tree was grown in the same manner as above.

Night Surveys

We used paired sample t-tests to compare murrelet density between T6-T9 and T15-T16 for both night and day, and to compare murrelet density for T6-T9 day *versus* night and T15-16 day *versus* night. We made the same comparisons for echosounder prey schools and prey relative abundance to explore possible spatial and diurnal prey differences. Because the data did not meet the requirements for parametric tests, we compared depth of prey schools between night and day using a Mann-Whitney U test.

Spatial Scale of Clustering

The Ripley's K statistic (Ripley 1981) tests whether spatial distributions of points depart from a random distribution to a clustered (aggregated) or regular distribution (Cornulier and Bretagnolle 2006). The K statistic can be used to describe whether spatial clustering exists and at what spatial scales. Because our study area is narrow (100m wide), and long (several kilometers), we treated the data as 1-dimensional. The transects were not straight (see Figure 1), which may cause an overestimation of the distance between murrelets in 2 dimensions, however Ripley's K has been applied to similar transects (angled or parallel) in other studies (*e.g.*, Burger *et. al.* 2004). Because we are treating the transect as 1-dimensional, distance between birds are based on the path traveled by the transect rather than the actual 2-dimensional distances. Details of this statistic and its uses have been described elsewhere (*e.g.,* Ripley 1981, O'Driscoll 1998, Burger *et al.* 2004, Wiegand and Moloney 2004).

Univariate - We calculated Ripley's K in MatLab (R2007B) using routines developed by O'Driscoll (1998) for all transects (T1-T11, T6-T9, T12-T16), and we compared patch length and crowding values among the three transect types using the Kruskal-Wallis test statistic. The transects were treated as one-dimensional rather than two-dimensional to avoid large edge effects. We did not control for spatial heterogeneity because we were interested in detecting clusters rather than explaining why clusters occur. We compared patch length and crowding among breeding periods using a Kruskal-Wallis test for transects T6-T9. Outliers were defined as values more than twice the standard deviation, and were filtered from the analysis.

To examine the effect of prey abundance on the spatial distribution of murrelets, we divided prey relative abundance and prey schools each into three categories of equal size (relative abundance [pixels$\cdot$km^{-1}]: low < 1.47, medium 1.47-2.73, and high > 2.73; prey schools [schools$\cdot$km^{-1}]: low < 0.56, medium 0.56-0.70, and high > 0.70) and used a Kruskal-Wallis test to detect differences in crowding and patch length for each dependent variable. Crowding is a measure of the aggregation (the number of murrelets in the patch) at that scale. The patch length, or characteristic spatial scale of clustering, is defined as the first significant peak of clustering and represents the distance between significant clusters. To avoid labeling small fluctuations as the patch length, we used the approach of O'Driscoll *et al.* (2000) and defined the patch length as the scale at which aggregation was higher than the next three successive values.

Bivariate - In addition to the univariate analysis, we ran a bivariate K statistic analysis of murrelet distribution with relation to prey for T6-T9 (N = 20). Bivariate routines were based on O'Driscoll (1998). We examined four parameters that describe how murrelets track prey for each survey date: (1) minimum scale of aggregation; (2) patch length; (3) crowding; and (4) significant aggregation proportion. The minimum scale of aggregation is the first scale at which aggregation is higher than the 99% confidence interval defined by a Monte-Carlo technique. Thus, the minimum scale of aggregation is the finest significant scale that murrelets can track prey. Patch length and crowding are defined above. Significant aggregation proportion is defined as the proportion of the total transect length (14.4 km), divided into 100 m intervals, that had significant aggregation. Significant aggregation proportion represents the range of scales that murrelets track prey.

We compared the four parameters describing spatial distribution outlined above to six independent variables: murrelet density, group count, prey schools, prey relative abundance, mean murrelet group size (defined as murrelet count divided by murrelet groups), and breeding period. Data were not normally distributed so we used non-parametric routines to test for significant differences. A Kruskal-Wallis test was used to detect differences between multiple groups, and a Mann-Whitney test between two groups. If the Kruskal-Wallis test was significant, a Mann-Whitney test identified *post-hoc* which values differentiated themselves in a pair-wise comparison. All groups were defined using 50% percentile for two groups and 33% percentiles for three groups, except breeding periods (defined above, Table 1). Only prey relative abundance was split into three groups, to detect if there was a maximum response at medium values, as suggested by Vlietstra (2005).

RESULTS

We sampled 8,890 birds on the at-sea strip transects with murrelets making up 93% of all bird species observed (Table 2). Murrelets were predominantly found in pairs (Figure 2).

Prey Sampling

We caught ten fish species and four zooplankton prey types that are known murrelet prey (Table 3). We dip-netted fish at 20 forage flocks with murrelets present during the season (mean count per flock = 23, SD = 21); all were adult capelin (*Mallotus villosus*; mean fork length = 84.3 mm, SD = 13.8 mm).

Of all the fish sampled by beach seine, 29% were juvenile salmonids (mean length = 65 mm, SD = 23 mm) and salmonids were present at 12 of the 14 sites sampled. Salmonid species included: chum (*Oncorhynchus keta*), pink (*O. gorbuscha*), chinook (*O. tshawytscha)*, sockeye (*O. nerka*), and coho (*O. kisutch*). When we switched to a beach seine with smaller mesh size on 14 July we began catching newly recruited Pacific sand lance (*Ammodytes hexapterus*; 4 sites, N = 37, mean fork length = 48.5 mm, SD = 4 mm) and capelin (2 sites, N = 36, mean fork length = 36 mm, SD = 7 mm).

Plankton samples showed high variation and sample sizes were not large enough to test whether significant differences in euphausiid and amphipod concentrations existed between T6-T9 and T15-T16 (Table 4). The high variation seen may be a result of the short nights, which resulted in rapid change of light levels over the sampling period. Paired sampling for euphausiids for the two regions was inconclusive because sampling was limited.

Fine-scale habitat use

Univariate analysis – At the 100 m bin scale, both murrelet density and group count were negatively correlated to depth, and distance to shoreline, creeks and flyways (Table 5). Prey variables were also negatively correlated with distance to shoreline, creeks, and flyways. Murrelet presence-absence showed similar relationships with independent variables as did murrelet continuous variables (Table 6, Figure 5).

CART analysis – Distance to flyways was the most important variable for almost every scale for each dependent variable (Figure 6). For the continuous dependents (murrelet density and group count), flyways became less important at the 1600 m scale and distance to other creeks became the most important variable. Prey relative abundance and prey schools became more important as bin size increased.

The final tree for murrelet abundance at the 100 m bin scale did not produce any nodes and therefore did not grow. The trees for murrelet group count and presence-absence grew two and eight nodes, respectively (Figure 7). These trees showed similar results as the analysis of importance values. For both trees, the first split was based on distance to flyways, on a split of about 9.6 km. There were more murrelet groups and murrelets were present more often within 9.6 km from the major flyways. The murrelet group count tree terminated without any further splitting, however the presence-absence tree was split further with distance to creeks. The univariate analysis showed murrelet group count to be negatively correlated with distance to creeks (*i.e.*, murrelet group count was higher closer to creeks). The classification tree showed that for murrelets close to flyways there was a higher proportion of murrelets present at a distance greater than 2 km from the nearest creek. Node 3 was further split based on depth with murrelet present in higher proportions in shallower water (bins with mean depth < 655 m). Node 5 was further split with the distance to flyways variable with murrelets being present in higher proportions further from major flyways (bins < 3.1 km from flyways). Generally, splits closest to the parent node (node 0) are the most generalizable (Rejwan *et al.* 1999). Although the presence-absence tree was grown beyond the first split, the improvements to the overall model from subsequent splits were far less (an order of magnitude less) than the first split and should be interpreted with caution.

Assessing the performance of trees built for the 100 m bin scale, the regression tree built with murrelet group count performed extremely poorly, explaining only 9.3% of the variance. The classification tree showed a 72.3% classification rate based on the test sample.

Meso-scale habitat use

Univariate analysis – We found no significant correlations between independent and dependent continuous variables other than the expected correlations between murrelet density and group count, and prey relative abundance and prey schools (Table 7). We found a significant difference in mean murrelet density among breeding periods (Kruskal-Wallis, N = 23, H = 9.7652, df = 2, p = 0.008, Figure 8). *Post-hoc* comparisons showed that the chick rearing and post-breeding period had significantly lower counts than incubation period (Z = 3.1192, p = 0.005).

No overall difference in murrelet densities existed among the four TOD categories (Chi-square = 4.896, df = 3, p = 0.108), however, when TOD was grouped into two categories, murrelet density was significantly higher during afternoon-dusk compared to dawn-morning (Z = -2.195, p = 0.028; Figure 9). No significant relationships were detected between dawn-morning and afternoon-dusk for prey schools (U = 38.5, Z = -0.7329, p = 0.473) or prey relative abundance (U = 41.0, Z = -0.5401, p = 0.624).

We found a significant overall difference in murrelet density among tide heights (Kruskal-Wallis, H = 8.647, N = 45, p = 0.034), however *post-hoc* comparisons among tide heights did not show any significant paired differences. When tidal stage was grouped into slack and rise/fall categories we found a significantly higher murrelet density (U = 28.0, Z = -2.0656, p = 0.040) and relative prey abundance (U = 5.0, Z = -3.2203, p = 0.001) during slack tides (Figure 10). We did not find a significant relationship between prey schools and the collapsed tidal stages (U = 27.5, Z = -1.3660, p = 0.177).

CART analysis – Both murrelet density and group count trees were first split based on prey relative abundance, with murrelets being more abundant and having higher group counts on transects where prey relative abundance was high (Figure 11). When the prey relative abundance was higher, murrelet density almost doubled compared to when it was low (210 *versus* 110 murrlets$\cdot$km^{-2}, respectively). Note that prey relative abundances are values based on specific equipment and collection protocol, thus values cannot be directly compared to other studies. Although both trees were split on similar values of the same variable, the improvement to the murrelet density tree was much larger compared to the improvement to the murrelet group count tree. The murrelet density tree was further split based on breeding period which again showed a relatively large improvement value. When breeding period was (1) nest initiation or (2) incubation, murrelet densities in T6-T9 were higher compared to (3) chick rearing and post breeding.

Between the two regression trees, the tree for murrelet density performed the best, explaining 48.9% of the variance in the training dataset while the regression tree for murrelet group count explained 24.5% of the variance.

Night Sampling

Murrelet densities varied significantly between regions at night and within regions between night and day (Figure 3). Comparing between sections, at night T15-T16 had significantly larger murrelet densities than T6-T9 ($t = -3.668$, $df = 5$, $p = 0.014$), however T6-T9 had significantly higher densities during the day ($t = 4.107$, $df = 5$, $p = 0.009$). Comparing directly between day and night samples within each section, T6-T9 had significantly higher densities during the day ($t = -5.426$, $df = 5$, $p = 0.003$) while T15-T16 had significantly higher densities during the night, ($t = -3.597$, $df = 5$, $p = 0.016$).

We did not find significant differences in prey schools or prey relative abundance between T6-T9 and T15-T16 at night (schools: $t = 0.266$, $df = 4$, $p = 0.803$; relative abundance: $t = 2.456$, $df = 4$, $p = 0.070$). Comparing between night and day, T6-T9 had significantly larger prey schools and prey relative abundance in the day than at night (schools: $t = -3.644$, $df = 4$, $p = 0.022$; relative abundance: $t = -5.098$, $df = 4$, $p = 0.007$). The prey schools or prey relative abundance for T15-16 did not differ significantly between day and night periods (schools: $t = -1.016$, $df = 4$, $p = 0.367$; relative abundance: $t = -1.199$, $df = 4$, $p = 0.297$). Prey schools were significantly shallower at night ($U = 2567$, $Z = -5.104$, $p < 0.001$; Figure 4).

We also observed large numbers of forage fish breaking the surface of the water as the spotlight passed over, appearing as though the light startled fish at the surface. This phenomenon was commonly seen throughout the night transects, generally for 10 to 100 m stretches of transect, most frequently near the shoreline. We dipnetted one sample of fish ($N = 3$) exhibiting this behavior and identified them as Capelin.

Spatial Scale of Clustering

Univariate - All transects showed significant clustering in the distribution of murrelets (Table 8). The three transect types showed slightly different values for patch length and crowding, however these differences were not significant (patch length Chi square = 4.06, $df = 2$, $p = 0.131$; crowding Chi square = 4.02, $df = 2$, $p = 0.134$).

Among breeding periods, crowding was not significantly different (Kruskal-Wallis; $H = 2.214$, $df = 2$, $p = 0.331$) but patch length differed significantly (Kruskal-Wallis; $H = 7.229$, $df = 2$, $p = 0.027$). *Post-hoc* comparisons showed that the chick rearing and post-breeding period (category 3) had a significantly larger patch length than the nest initiation (category 1, Z = 2.684, p = 0.007) and incubation periods (category 2, Z = 2.052, p = 0.040). There was no significant difference between nest initiation and incubation periods.

Prey schools (mean ± SD = 0.69 ± 0.33 schools·km^{-1}) yielded no differences in crowding (Kruskal-Wallis; H = 0.599, df = 2, p = 0.741) or patch length (Kruskal-Wallis; H = 0.283, df = 2, p = 0.868) among high, medium, and low categories. Prey relative abundance (mean ± SD = 2.99 ± 2.85 pixels·km^{-1}) likewise yielded no differences in crowding (N = 19, H = 0.942, df = 2, p = 0.624) or patch length (N = 19, H = 0.642, df = 2, p = 0.725).

Bivariate – Days with high mean murrelet group size (mean group size > 2.33 murrelets·group^{-1}) had significantly lower minimum significant scale (*i.e.*, the smallest scale at which murrelets can track prey) compared to days when group size was one to two birds (Mann-Whitney; U = 11.5, Z = -2.494, p = 0.013; Table 9, Figure 13). Days with high mean group size also had significantly lower patch length (Mann-Whitney; U = 14.5, Z = -2.298, p = 0.022; Table 9, Figure 13). When comparing among prey relative abundance categories (low, medium, high, Kruskal-Wallis; H = 9.199, df = 2, p = 0.010), days with medium relative prey abundances yielded a significantly higher significant aggregation proportion than low and high values which did not differ significantly from each other (Figure 14).

DISCUSSION

Prey Sampling

Capelin were the only prey present in mixed-species forage flocks in PS. Murrelets in the forage flocks were seen foraging directly around capelin concentrated at the surface. Anecdotally, foraging flocks were commonly seen in our study region. We also found capelin larvae (40 ± 7 mm) in beach seine and plankton tow samples as well as newly settled and adult capelin in the dipnet samples of forage flocks. The presence of larval and newly-settled capelin likely indicated spawning activity (Brown 2002). Capelin form spawning congregations in nearshore regions of Alaska during late spring/summer (Arimitsu *et al.* 2007, 2008) and generally inhabit cooler waters with lower primary productivity compared to Pacific herring (*Clupea pallasii*) and sand lance (Arimitsu *et al.* 2007). These spawning concentrations of capelin are known to support predator populations during periods when predators are energetically constrained (Davoren *et al.* 2002, Womble *et al.* 2005). If capelin use PS as a spawning region, they may occur at high enough concentrations to provide murrelets with a reliable source of prey throughout the breeding season which is supported by the frequency at which we found capelin at the feeding flocks.

Salmonids were found in high frequency in the beach seine samples and were often noted schooling close to shore (within 1 - 3 m of water depth) within PS. The release of juvenile salmonids from the hatchery at Speel River may cause elevated concentrations in the nearshore. Salmonids have been found in the diets of murrelets (Burkett 1995) and because of their ubiquity in the nearshore in our study region, they are likely taken as prey.

Sand lance are often found in high abundances in nearshore waters associated with specific sediments found in the intertidal and subtidal regions (Ostrand *et al.* 2005, Haynes *et al.* 2007, in press). Compared to other regions (*e.g.,* Speckman *et al.* 2003, Arimitsu *et al.* 2007, Haynes *et al.* 2007, in press), sand lance were not found in high abundance in PS. We sampled all shorelines that could be sampled with a beach seine, however we only found a total of 74 sand lance at seven sites from 17 sampling events. Areas where sand lance are more common in Alaska (Robards *et al.* 1999, Speckman *et al.* 2003, Ostrand *et al.* 2005, Arimitsu *et al*. 2007) and in British Columbia (Haynes *et al*. 2007, in press) generally have more shallow nearshore regions and sandy intertidal habitat available. The lack of abundant sand lance in our study area may be due to the deeper fjord habitat of PS lacking suitable intertidal and shallow subtidal habitat that sand lance use for burying or spawning. The presence of newly recruited sand lance suggests that recruitment of larval sand lance occurs to some degree in PS. However, if this recruitment was substantial we would have likely seen considerably more of the larger size classes of sand lance during sampling.

Other species of murrelet prey found in PS included: Pacific sandfish (*Trichodon trichodon*), dolly varden (*Salvelinus malma malma*), walleye pollock (*Theragra chalcogramma*), and zooplankton species (euphausiids, amphipods, mycids and chaetognatha). The presence of these species is important to document, however the relative importance of the different prey types is difficult to assess without further investigation. Pacific herring were notably absent in PS based on our sampling and are unlikely to be found within our study region (D. Csepp, pers. comm. 2008). Juvenile herring have been found to be extremely important for murrelets in other regions of AK (*e.g.*, Kuletz 2005) and are considered one of the most important prey items for murrelets across their range (Burkett 1995).

Fine-scale habitat use

At the various scales of analysis, the most important variable to murrelet distribution was distance to flyways, with murrelets remaining close to major flyways. Murrelets fly inland to nest sites, often multiple times per day depending on the breeding stage and thus congregate in marine regions adjacent to inland flyways as staging grounds for their inland flight (Nelson 1997).

Results from CART trees at the 100 m bin scale suggested that murrelets were more likely to be found within about 9.6 km of the flyways and the number of murrelet groups were higher within this distance as well. A range of 9.6 km from each major flyway encompasses a large portion of the study area, therefore murrelets may just be staying on the “inside” of PS and not using the area close to Steven’s Passage.

All three major flyways in this study were also estuarine areas. Murrelets have been associated with estuarine habitat in other regions (Miller *et al.* 2002, Yen *et al.* 2004 and Ronconi 2008). Yen *et al.* (2004) suggest that this positive correlation arises because of the unique aquatic characteristics that estuaries provide for murrelets. Although this may be the case, estuaries may also be areas where murrelets congregate because in mountainous areas, estuaries provide entrances to major watersheds, which in turn provide natural flyway corridors through inland terrain to nesting habitat (*e.g*., Burger 1997). Thus, in addition to using estuaries for foraging habitat, murrelets may be found close to estuaries during breeding because they are often used as staging grounds for inland flights.

Although distance to flyways was generally the most important variable, as the scale increased to 1600 m flyways became less important relative to other continuous dependent variables. For both murrelet density and group count, distance to creeks became the most important variable, followed by prey relative abundance. Based on the classification tree for murrelet presence-absence for the 100 m bin scale, birds were more likely to be present at distances greater than 2 km from the nearest creek suggesting that there may be an interaction effect between creeks and flyways. This is opposite to the univariate analysis results that showed that murrelets were found closer to creeks. Distance to creeks was significantly correlated with distance to flyways (*i.e.,* flyways also were major watersheds and therefore were also considered “creeks”). Thus, the univariate negative correlation between murrelet density and group count and distance to creeks may be related to the covariance of distance to creeks with distance to flyways. In two recent studies on murrelet habitat use in British Columbia, Ronconi (2008) and Barrett (2008) found that distance to old-growth nesting habitat was one of the most important variables determining habitat selection during breeding season. Another variable seen important in both studies (Barrett 2008, Ronconi 2008) was distance to “beach” habitat which is generally linked with sand lance habitat (Haynes *et al.* in press). Here, such habitat was scarce, thus the lack of sand lance seen within our study region during prey surveys.

Similar to other studies (Logerwell and Hargreaves 1996, Fauchald *et al.* 2000, Fauchald and Erikstad 2002), our study demonstrated the difficulty of linking seabird distributions with prey observations at fine scales. Difficulties arise due to mismatch between echosounder data, actual prey densities, and densities of birds on the surface. Echosounders sample only a portion of the water and therefore only a portion of the prey within the transect. This sampling mismatch is most prominent at fine scales and though we chose a relatively narrow strip transect width (100 m) mismatches between echosounder observations, actual fish densities, and bird densities are unavoidable using these survey methods.

The regression tree for murrelet group count at the 100 m bin scale explained only 9.3% of the variation and the tree for murrelet density failed to grow at this scale. This suggests that variables used in the modeling process lacked the ability to explain murrelet habitat use patterns based on abundance data (*i.e.*, murrelet density or group count). Abundance models have generally been less precise than occupancy models given the inherent difficulties in modeling count data (Stauffer 2002). The classification tree model for murrelet presence-absence performed better with the tree classifying 72.3% of the bins correctly for the test dataset. However, considering that the data used to build the model had a presence-absence ratio of about 50:50, a model which chose to classify all sites as either “present” or “absent” would have a 50% classification rate. Thus, the classification tree had a classification improvement of 22.3% compared to a model that classified all bins as only one of the binary categories.

Meso-scale habitat use

Prey relative abundance was the most important variable at the meso-scale for both murrelet density and group count. Although prey schools and prey relative abundance were not important at the fine scale, the importance value analysis showed that they became more important as bin size increased. Thus, based on the fine scale analysis, it is predictable that prey schools or relative prey abundance would be important at this larger scale of analysis.

Breeding season was the second most important variable in the murrelet abundance tree. When prey relative abundance was low, murrelets were more abundant during nest initiation and incubation, compared to after 13 July during chick rearing and post-breeding dispersal. PS has three important flyways and numerous minor flyways into nesting regions (Nelson *et al.* 2008). When murrelets are incubating, they must remain close to the inland nesting areas. Thus, murrelets using nesting habitat in PS remain within the study area even when prey availability is low. When murrelets enter post-breeding, they are no longer required to remain close to the nest and can forage elsewhere when prey availability is low in the region. Although the category also includes chick rearing, which would require murrelets to stay close to PS, the post-breeding lack of attachment to PS may be driving the relationship between low murrelet numbers and low prey availability for this category. Speckman *et al.* (2000) found that the chick rearing/fledgling category had the highest variability with regards to murrelet at-sea densities, which again may have been driven by post-breeders using the region only when the prey availability was high. Becker and Beissinger (2003) found that murrelets stayed close to nesting habitat when prey availability was high and moved to cooler waters (“higher quality foraging habitat”) when prey availability was low. Conversely, Burger *et al.* (2008) found that distance to nesting habitat was not important in structuring murrelet distribution at-sea, however, prey availability was not considered. We found low prey availability was associated with lower murrelet densities, however, the interaction effect between low prey availability and breeding stage suggests that murrelets still remain close to nesting habitat when prey abundance is low during the breeding season. Murrelets are energetically constrained and thus may be less likely to make longer trips to find better foraging habitat. However, murrelets may remain around PS for other reasons, for example, to stage for inland flights after having foraged elsewhere thus accounting for the differences between the breeding and post-breeding periods.

Due to the inherent noise of the systems, modeling abundance data in ecology can be difficult (Stauffer 2002). This being considered, the model of murrelet density for T6-T9 performed extremely well, with the regression tree based on two independent variables explaining almost 50% of the variation. The ability to explain this amount of variation suggests that at this scale, unlike the finer scales examined above, prey observations from echosounder recordings (coupled with the variation explained by breeding period) are useful in describing murrelet distribution. Note that although models performed well, trees were built based on only 25 survey days (N = 25) which is a relatively small sample size for CART analysis.

The foraging activity of piscivorous seabirds has been linked to tidal cycles (Holm and Burger 2002, Zamon 2003). The nature of the relationship between the tidal cycle and seabird foraging is likely dependent on the specific physical characteristics of the region as well as the bird species involved (*e.g.*, Holm and Burger 2002). Although tidal stage was not selected in the tree analysis, it was found to be related to murrelet densities in the univariate analysis, with murrelets more abundant in the surveys at slack tide compared to rising/falling tide. The increase in murrelet densities during slack tide was also accompanied by significantly higher prey abundance. The tidal cycle likely makes prey more available by concentrating prey and providing favorable foraging conditions (Holm and Burger 2002). Holm and Burger (2002) found similar results with piscivorous seabirds preferring slack or moderate tidal currents to forage. Speckman *et al*. (2000) also found that murrelet numbers peaked during slack tides, but they also increased during falling morning tides in Auke Bay, AK.

TOD was also not selected for in the tree models, however we did find that murrelet densities were highest during afternoon-evening compared to dawn-morning. This is contrary to what was found by Speckman *et al.* (2000) and Carter and Sealy (1990) who found that murrelet densities were highest in the dawn-morning and diminished into the evening-dusk in their respective study regions. Note that the TOD differences seen in our study were not related to prey abundance and thus may have been related to social or breeding behavior rather than foraging.

Night Sampling

Murrelets used habitat differently in light and dark periods. Based on our surveys, we found that murrelets transition from the shallower, sheltered waters of the inner transect, used during the day, to more exposed, deep and open water outer transect during dark hours. This was also documented by data loggers and visual surveys in PS by Newman *et al.* (2006) and Nelson *et al.* (2007, 2008).

Little is known about Marbled Murrelet spatial distribution and behavior at night. In

California, Peery *et al.* (in press) found that murrelets move a few km away from daytime feeding areas at night. In Auke Bay, Whitworth *et al.* (2000) noted murrelets moving away from shore and into deeper waters nightly. In Desolation Sound, British Columbia, murrelets moved away from shorelines and out of narrow channels where they occur in high abundance during the day to deeper open waters at night (Lougheed 2000). The results from these studies parallel what we saw in our study region.

Our results suggest that murrelets are not redistributing themselves in response to a diurnal change in prey abundance. We did not find significant differences in echosounder values of prey schools or prey relative abundance between regions suggesting that differences in the distribution of murrelets between regions at night were not due to differences in prey availability. When comparing within regions, T15-T16 did not differ between night and day, but T6-T9 had higher prey schools and prey relative abundance during the day. However, we consistently observed large numbers of forage fish breaking the surface of the water as the light spotlight passed in the T6-T9 region and to a lesser extent T15-T16. The high abundance of fish (likely capelin) at the surface, along with significantly shallower prey schools on the echosounder, suggest that capelin move to surface waters during the night. If capelin are close to the surface, they would not be seen on the echosounder because it does not record the upper few meters of water, thus explaining the reduced number of prey schools in the T6-T9 region at night. Using telemetry, Jodice and Collopy (1999) and Peery *et al.* (in press) found that murrelets in Oregon and California, respectively, did not dive at night. Thus, it is unlikely that murrelets redistribute themselves to forage nocturnally.

Moving to the mouth of PS may provide murrelets with open water where they can rest without risk of drifting into shore and avoid predation (Lougheed 2000). A significant part of the murrelet's life-history and behavior has evolved around predator avoidance including, but not limited to, their cryptic plumage, crepuscular inland flights, and secretive behavior at nest sites (Nelson and Hamer 1995). Although little is known about possible nocturnal predators of murrelets, Snowy Owls have been known to target Ancient Murrelets (*Synthliboramphus antiques*) in Alaska (Williams and Frank 1979) and Great Horned Owls (*Bubo virginianus*) have been seen taking Rhinoceros Auklets (*Cerorhinca monocerata*) off the water in Washington (Hayward *et al.* 1993). Some murrelets are thought to move to offshore wintering grounds just before their pre-basic molt (Carter and Stein 1995); this could be associated with avoiding predation in addition to finding locations with readily available prey. Murrelets may also be gathering for social interaction with other murrelets at night in the area. Speckman *et al.* (2003) suggested that many of the behavior patterns of murrelets (displaying, pair bonding, choosing mates, foraging) are socially facilitated. Certainly, more research is needed to determine the mechanisms that drive murrelet offshore at night in Southeast Alaska.

Although we compared day to night counts directly, survey techniques are different because night surveys require spotlights and thus may underestimate the number of murrelets due to larger numbers of undetected birds. During day transects, murrelets that flush before the vessel can easily be seen from a long distance. At night, the distance illuminated by the beam of the spotlight does not allow the detection of birds that flush at as great a distance. However, murrelets are less likely to flush at night, which makes murrelets captures possible at night but not during the day (Whitworth *et al.* 1997). Thus, numbers counted at night may be comparable to day surveys.

Spatial Scale of Clustering

Univariate - Results from Ripley's K can reveal spatial structure and thus give guidance to appropriate scales of study (O'Driscoll 1998). At the smallest spatial scale, murrelets are known to forage mainly in pairs during breeding season (McFarlane Tranquilla *et al.* 2003), which was also seen in this study. At the scale of kilometers, Ripley's K analysis revealed that murrelets clustering was highly variable, with patch length ranging from 300 m to over 9 km. Mean patch length was between 1.84 and 3.96 km depending on the transect, which is slightly higher than the value of 1 ± 0.9 km for offshore waters of Vancouver Island (Burger *et al.* 2004), but lower than the 9.18 ± 2.30 km reported for nearshore waters of the Vancouver Island (Burger *et al.* 2008).

Patch length increased significantly during chick rearing and post-breeding. Again, this is likely due to post-breeding birds no longer being energetically or spatially constrained (*i.e.*, not required to stage in PS before making inland flights). The increase in patch length after breeding suggests that murrelet groups are foraging further from one another. As more birds enter post-breeding, flyways become less important and murrelet groups can be distributed more evenly within the study area, thus increasing patch length.

No distinction was made between first order and second order clustering in this analysis. Instead, we were interested in determining whether clustering existed and at what scales. Thus, variations in the clustering of murrelets may be a response to variations in environmental characteristics (first order) or may reflect variations in interaction behavior among murrelets such as competition or social groupings (second order; Cornulier and Bretagnolle 2006).

The Ripley's K statistic assumes that all sample counts along transects be taken from the same statistical distribution, independent of time and space (O'Driscoll 1998). This assumption of stationarity is likely not the case because seabirds distribute themselves relative to rapidly changing environmental conditions. However, in a similar spatial analysis of seabird distributions, O'Driscoll (1998) assumed that the seabird distribution was weakly stationary as was the case in this study. Because transects here are essentially spatially 1-dimensional (*i.e.,* long and narrow), patch length and clustering are not true measures of overall patch dimensions. Also, we did not perform any edge correction and thus higher patch lengths are likely less accurate than low values (O'Driscoll 1998).

Bivariate - Seabirds are known to congregate at areas with high prey concentration (Fauchald and Erikstad 2002, Piatt *et al.* 2006). However, many studies have had little success linking the distribution of seabirds to the distribution of their prey (*e.g.*, Hunt *et al.* 1992, Logerwell and Hargreaves 1996, O'Driscoll 1998, Fauchald *et al.* 2000, Skov *et al.* 2000). Many of those that have linked seabird distributions to prey have found that the existence of the relationship has been spatially or temporally inconsistent (*e.g.*, Schneider and Piatt 1986, Wright and Begg 1997, Vlietstra 2005). For example, Burger *et al.* (2004) found that pooled alcids (including Marbled Murrelets) were significantly associated with prey during 67 % of the transects based on a Ripley's K analysis. We found both spatial and temporal inconsistency with how murrelets tracked prey. Although inconsistent, murrelets generally tracked prey at some scale on each study day (18 of the 20 days) and tracked prey down to the finest scale of analysis (100 m) for 8 of those 18 days. This suggests a relatively close temporal-spatial relationship between murrelets and their prey even though variation in this tracking exists. Based on telemetry observations, murrelets are using PS as a flyway to inland nesting sites around the area (Nelson *et al.* 2008). The high concordance between murrelets and their prey demonstrate that they also use this area for foraging.

Swartzman and Hunt (2000) found that larger clusters of murres (*Uria* spp.) and puffins (*Fratercula* spp.) were more consistently associated with prey. Their results suggest a positive relationship between size of the cluster (*i.e.*, number of birds in a "group") and the strength of the association with prey. In our study, murrelets were most commonly found in groups of two. However, on days when murrelets formed larger groups (mean >2.33 murrelets$\cdot$group^{-1}), the groups were associated with prey at a finer scale (smaller minimum scale of aggregation). This finer scale of aggregation suggests that when murrelets are in larger groups they may be more closely tracking prey (*i.e.*, aggregating at prey schools). This result was accompanied with a significantly smaller patch size on days where the mean murrelets group size was > 2.33 murrelets$\cdot$group^{-1}. Because large groups were more closely associated with prey schools, they were more likely to be close to each other (shorter patch length).

The scale at which a predator tracks its prey reveals the amount of concordance between the two and provides insight to foraging energetics (Davoren *et al.* 2002). Further, the regional abundance of prey can influence the tracking scale (Vlietstra 2005). We found significant differences in the scales over which murrelets can track their prey which appeared to be related to prey abundance. Murrelets tracked prey over the largest range of scales (*i.e.*, significant aggregation proportion) when moderate levels of prey were available. This fits the non-linear relationship described by Vlietstra (2005). When prey is very abundant, it is not energetically efficient to track the prey, and birds might employ a “sit-and-wait” approach. At intermediate prey levels, birds would be expected to distribute themselves according to ideal free distribution, displaying a high concordance between predator and prey. However, at even lower levels, there are likely many factors that may limit a predator’s ability to track prey, including lack of information on prey patches (Vlietsra 2005) or limits in activity budgets (Ronconi and Burger 2008). Regardless of prey abundance, environmental and behavioral factors, such as fluctuations in physical cues (Schneider 1982) or interspecific competition (Burger *et al* 2008), the scale at which a seabird can track its prey may be limited and thus complicate the relationship between prey abundance and tracking scale. For example, Becker and Bessinger (2003) found associations between murrelets and prey only when prey levels were low, regional upwelling was low, and sea surface temperature was high. Here, murrelets showed a larger range of aggregation when prey was at moderate levels suggesting they tracked prey more closely, however, they were not tracking prey at significantly finer scales, as might be expected.

Applications for Management and Conservation

Top predators rarely occur in high densities in the marine environment, however, when they do, they have the potential to have top down effects on the ecosystem at a regional scale. (Hunt and McKinnell 2006). In our study region, murrelets occurred in relatively high abundances relative to other studies suggesting this region is an important area for murrelets. For example, our study region (T1-T16) had a mean density of 111 ± 35 murrelets$\cdot$km^{-2} whereas Agler *et al.* (1998) found overall densities of *Brachyramphus* murrelets (Marbled and Kittlitz's (*B. brevirostris*) murrelets) for Southeast Alaska to be 19.4 birds$\cdot$km^{-2}, but also found areas with densities > 150 birds$\cdot$km^{-1}. On the southwest coast of Vancouver Island, an area known to have some of the highest densities of murrelets in British Columbia (Burger 2002), Burger *et al.* (2008) found densities of 45.16 ± 10.08 murrelets$\cdot$km^{-2}. Given that murrelets are the numerically dominant seabird in the region and occur in high densities, it is likely that murrelets play an important role in ecosystem function as a top marine predator by shaping local prey distributions.

Understanding the activities of Marbled Murrelets at-sea is necessary in order to aid in conservation efforts for this species. Seabirds are conspicuous top predators which can act as biomonitors of marine ecosystems (Furness and Camphuysen 1997). Seabirds have been used as indicators of prey abundance (*e.g.,* Bertran and Kaiser 1993, Furness and Tasker 2000, Litzow *et al.* 2000) and the reproductive success of murrelets has been linked to the availability of prey (Becker *et al.* 2007). Here, modeling analyses show that murrelet densities are related to prey densities and murrelets can track prey down to very fine scales. This suggests that murrelets could be useful indicators of areas of high prey availability and high marine productivity.

Knowledge of distribution patterns of murrelets at-sea can provide information on how known anthropogenic impacts, such as disturbance from vessel traffic (Bellefleur *et al.* in press), mortality due to fisheries bycatch (Carter *et al.* 1995), or pollution such as oil spills (Carter and Kuletz 1995) may affect murrelets. Management of these impacts depends on knowledge of murrelet habitat use over varying temporal and spatial scales. For example, an oil spill response that concentrates efforts only in areas murrelets use during the day, which has been the focus of studies on murrelet habitat use, will miss areas where murrelets concentrate at night. In PS, murrelet distribution fluctuates dramatically between day and night hours with murrelets moving out of regions used heavily during the day. On a larger temporal scale, areas adjacent to flyways appear to be important during breeding. Murrelets are likely using these areas as staging grounds for inland flights. The Ripley’s K analysis suggests that as post-breeding begins, murrelets spread more evenly across the study area and these concentrations break up. Thus, seasonal protection or management of these areas may provide similar benefits to murrelets as yearlong protection. In addition to management efforts, future efforts to survey murrelet populations require similar information on marine distribution patterns in order to plan effective and accurate surveys.

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Tables:

Table 1. Definition of independent variables for statistical analysis.

		Categories		
Parameter	Definition	Low	Medium	High
Murrelet Density	Murrelets $\cdot$ km^{-2}	≤ 142	NA	> 142
Murrelet Group Count	Number of murrelet groups observed (groups $\cdot$ km^{-2})	≤ 58	NA	> 58
Mean Group Size	Total murrelet abundance/group count (murrelets $\cdot$ group^{-1})	≤ 2.33	NA	> 2.33
Prey Relative Abundance	Sum of prey echosounder target pixels (pixels $\cdot$ km^{-1})	< 1.47	1.47-2.73	> 2.73
Prey Schools	Number of prey echosounder targets (schools $\cdot$ km^{-1})	< 0.56	0.56-0.70	> 0.70
Breeding Periods	Based on Nelson *et al.* 2008		See Methods	

Table 2. Summary of species composition from at-sea transects in Port Snettisham.

	Daytime Transects		Nighttime Transects	
	Entire Transect (birds·km^{-2})	Transects 6-9 (birds·km^{-2})	Transects 6-9 (birds·km^{-2})	Transects 15-16 (birds·km^{-2})
Alcids				
Marbled Murrelet (*Brachyramphus marmoratus*)	111.04 ± 34.83	129.72 ± 77.46	14.61 ± 16.15	81.50 ± 77.42
Pigeon Guillemot (*Cepphus columba*)	0.51 ± 0.60	0.55 ± 2.09		
Common Murre (*Uria aalge*)	0.61 ± 1.31	0.03 ± 0.14		
Other species				
Unidentified Gull Species (*Larus spp.*)	1.96 ± 2.38	2.69 ± 6.23	4.69 ± 10.27	10.99 ± 20.76
Bonaparte's Gull (*Larus philadelphia*)	0.10 ± 0.21	0.75 ± 3.75		
Mew Gull (*Larus canus*)	0.19 ± 0.40	0.33 ± 0.78		
Scoter Species (*Melanitta spp.*)	0.22 ± 0.62	0.03 ± 0.14	0.10 ± 0.26	
Surf Scoter (*Melanitta perspicillata*)	1.59 ± 3.77		0.50 ± 1.31	8.79 ± 15.66
White Winged Scoter (*Melanitta fusca*)	0.32 ± 0.75			
Merganser Species (*Mergus spp.*)	0.07 ± 0.14		0.30 ± 0.79	
Common Merganser (*Mergus merganser*)	0.54 ± 1.51	0.69 ± 2.95		
Unidentified Loon Species (*Gavia spp.*)	0.10 ± 0.21	0.19 ± 0.47	0.10 ± 0.26	
Common Loon (*Gavia immer*)	0.19 ± 0.23	0.50 ± 1.83		
Pacific Loon (*Gavia pacifica*)	0.10 ± 0.15	0.11 ± 0.26	0.10 ± 0.26	
Unidentified Duck Species		0.11 ± 0.56	0.13 ± 0.34	
Goldeneye Species (*Bucephala spp.*)	0.05 ± 0.14	0.08 ± 0.42	0.10 ± 0.53	
Harlequin Duck (*Histrionicus histrionicus*)	0.02 ± 0.07	0.03 ± 0.14		
Red Necked Phalarope (*Phalaropus lobatus*)	0.05 ± 0.14	0.19 ± 0.97		
Arctic Tern (*Sterna paradisaea*)		0.03 ± 0.14		

Table 3. Inventory of species present in Port Snettisham that are known to be preyed upon by murrelets elsewhere.

Prey Type	Species	Sampling Method
Fish	*Mallotus villosus*	Beach Seine, Dip Net, Plankton Tow
	Oncorhynchus gorbuscha	Beach Seine, Dip Net
	Oncorhynchus keta	Beach Seine
	Oncorhynchus tshawytscha	Beach Seine
	Oncorhynchus kisutch	Beach Seine
	Oncorhynchus nerka	Beach Seine
	Ammodytes hexapterus	Beach Seine
	Salvelinus malma malma	Beach Seine
	Theragra chalcogramma	Beach Seine
	Trichodon trichodon	Beach Seine
Plankton	Euphausiid sp.	Plankton Tow
	Chaetognatha sp.	Plankton Tow
	Amphipod sp.	Plankton Tow
	Mycid sp.	Beach Seine

Table 4. Euphausiid and Amphipod counts for T6-9 and T14-16. Each number represents the sum of the four sample stations along each transect section.

	Euphausiids		Amphipods	
Date	T6-T9	T14-T16	T6-T9	T14-T16
1-Jul	35	15	26	99
9-Jul		285		119
14-Jul	75		148	
16-Jul		104		325

Table 5. Bivariate Spearman's correlation (r_s) of continuous dependent and independent variables. No adjustments were made to significance values for multiple comparisons.

	Murrelet Density	Murrelet Group Count	Prey Schools	Prey Relative Abundance	Tidal Slick	Distance to Creek	Distance to Flyways	Distance to Shoreline
Murrelet Group Count	.898(**)							
Prey Schools	.140(**)	.155(**)						
Prey Relative Abundance	.141(**)	.156(**)	.979(**)					
Tidal Slick	.018	.048	-.008	-.012				
Distance to Creek	-.118(**)	-.190(**)	-.096(*)	-.095(*)	.019			
Distance to Flyways	-.222(**)	-.259(**)	-.216(**)	-.197(**)	-.182(**)	.217(**)		
Distance to Shoreline	-.178(**)	-.292(**)	-.178(**)	-.179(**)	.013	.655(**)	.237(**)	
Depth	-.255(**)	-.275(**)	-.061	-.053	-.028	.249(**)	.285(**)	.150(**)

*Significant at the 0.05 level (2-sided)

**Significant at the 0.01 level (2-sided)

Table 6. Mann-Whitney U test results for the 100 m bin scale using murrelet presence-absence as the grouping variable.

Variable	U	Z adjusted	p-value
Prey Schools	15565.5	-2.705	0.007
Prey Relative Abundance	15501.0	-2.791	0.005
Tidal Slick	16419.0	-1.780	0.075
Creek	14393.0	3.254	0.001
Flyways	11814.0	5.683	<0.001
Shoreline	12365.0	5.164	<0.001
Depth (m)	12246.0	5.276	<0.001

Table 7. Bivariate Spearman's correlation (r_s) matrix for the T6-T9 CART analysis

	Murrelet Group Count (groups$\cdot$km^{-2})	Murrelet Density (murrelets$\cdot$km^{-2})	Tidal Slick$\cdot$km^{-1}	Prey Schools (schools$\cdot$km^{-1})
Murrelet Density (Murrelets$\cdot$km^{-2})	0.891(**)			
Tidal Slick$\cdot$km^{-1}	0.290	0.295		
Prey Schools (schools$\cdot$km^{-1})	0.297	0.181	-0.147	
Prey Relative Abundance (pixels$\cdot$km^{-1})	0.411	0.349	0.136	0.600(**)

*Significant at the 0.05 level (2-sided)

**Significant at the 0.01 level (2-sided)

Table 8. Patch length and crowding values from the Ripley's K analysis of murrelet spatial distribution.

		Patch Length (km)			Crowding (birds·patch^{-1})		
Transect	N	Mean	Standard Deviation	Range	Mean	Standard Deviation	Range
T1-T11	7	4.0	2.8	0.9-9.1	31	16	11-50
T12-T16	7	1.8	1.9	0.3-5.5	28	26	2-77
T6 - T9	20	2.0	1.4	0.5-5.1	18	14	3-48

Table 9. Statistical tests (Mann-Whitney between two groups, Kruskal-Wallis among three groups) for all four aggregation parameters, for all six independent variables. Results in bold are significant at the 0.05 level.

Parameter	Minimum Scale of Aggregation	Patch Length	Crowding (birds·patch^{-1})	Significant Aggregation Proportion
Range	0.1 to 4.1 km	0.1 to 4.8 km	0.86 to 88.80	0-13.2 of 14.4 km
Mean	0.92 km	1.58 km	15.08	4.63 km
SD	1.27 km	1.58 km	20.96	4.52 km
Murrelet Density	U = 19.0, Z = -1.730, p = 0.084	U = 21.0, Z = -1.445, p = 0.148	U = 33.0, Z =-0.289, p = 0.773	U = 31.5, Z = -0.795, p = 0.427
Murrelet Group Count	U = 29.5, Z = -0.281, p = 0.779	U = 31.5, Z = -0.434, p = 0.665	U = 28.0, Z = -0.770, p = 0.441	U = 38.5, Z = -0.177, p = 0.860
Mean Murrelet Group Size	**U = 11.5,** **Z = -2.493,** **p = 0.013**	**U = 14.5,** **Z = -2.298,** **p = 0.022**	U = 35.0, Z = -0.096, p = 0.923	U = 35.5, Z = -0.442, p = 0.659
Prey Schools	U = 25.5, Z = -0.730, p = 0.465	U = 25.5, Z = -1.012, p = 0.213	U = 31.0, Z = -0.481, p = 0.630	U = 37.0, Z = -0.309, p = 0.757
Prey Relative Abundance	H = 1.713 df = 2 p = 0.425	H = 2.061 df = 2 p = 0.357	H = 0.493 df = 2 p = 0.781	**H = 9.199,** **df = 2,** **p = 0.010**
Breeding Periods	H = 1.713 df = 2 p = 0.425	H = 2.061 df = 2 p = 0.357	H = 0.316 df = 2 p = 0.854	H = 2.125 df = 2 p = 0.346

Figures:

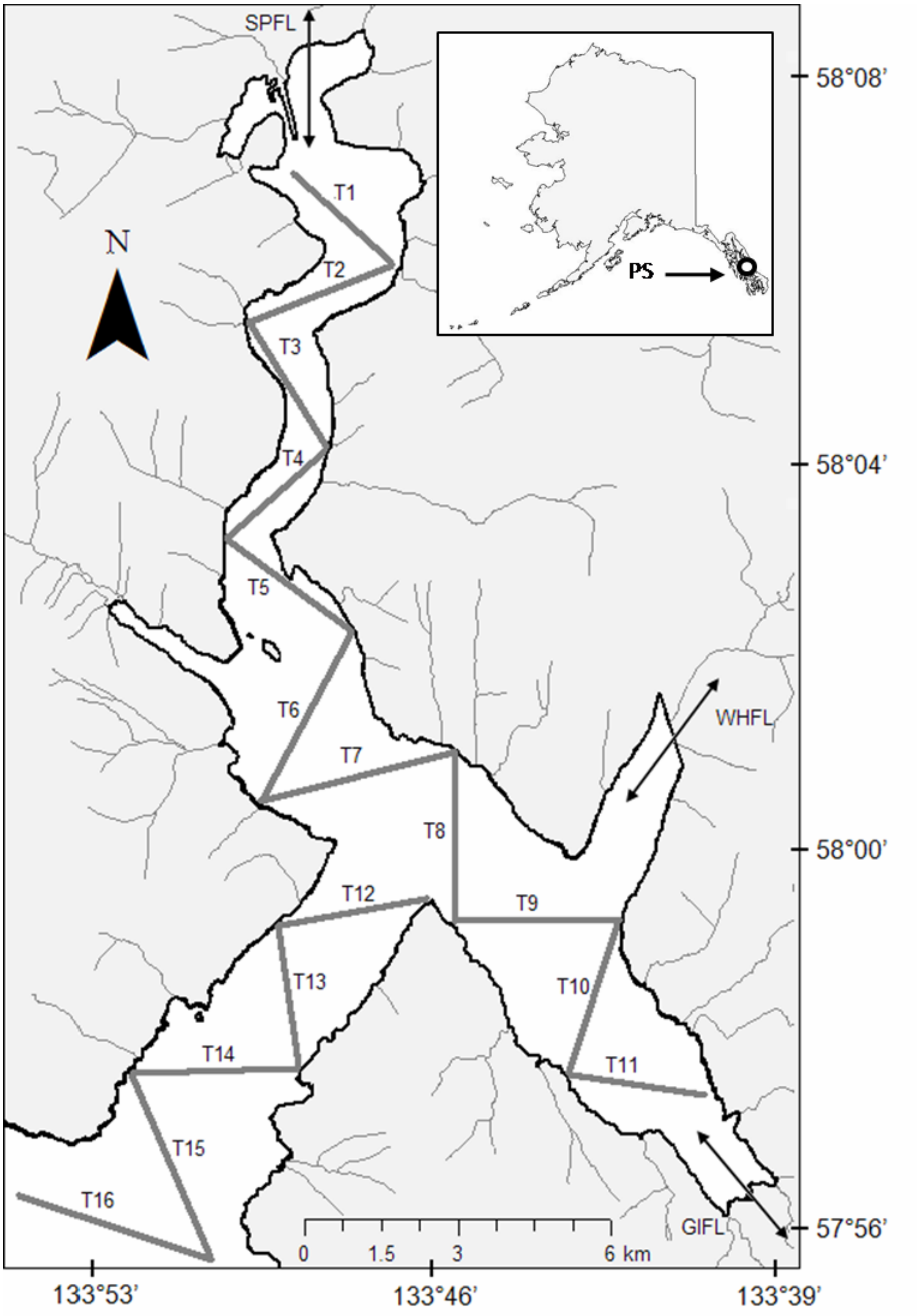

Figure 1. Transects used to survey the at-sea distribution of Marbled Murrelets in Port Snettisham, AK. Dark grey lines indicate transect route. Double-headed arrows indicate major flyways (GIFL = Gilbert Bay flyway, WHFL = Whiting River flyway, SPFL = Speel River flyway) for murrelets inland to nesting habitat. Numbers on the vertical and horizontal axes of the figure represent latitude and longitude respectively.

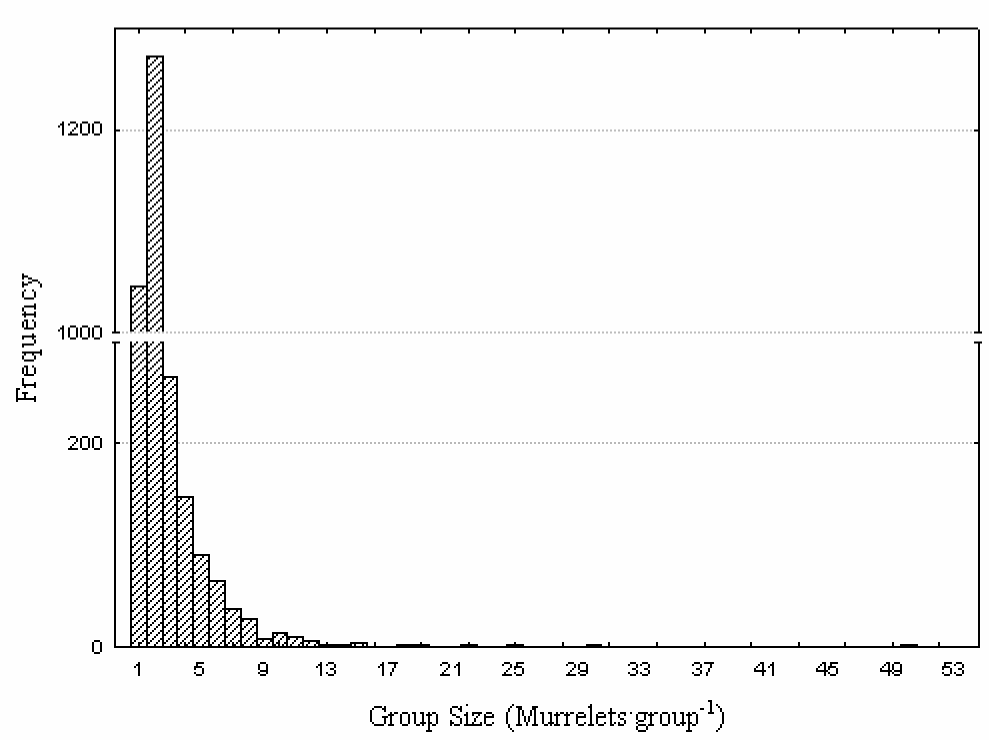

Figure 2. Histogram of murrelet group size from day transects (note the scale break between 300-1000).

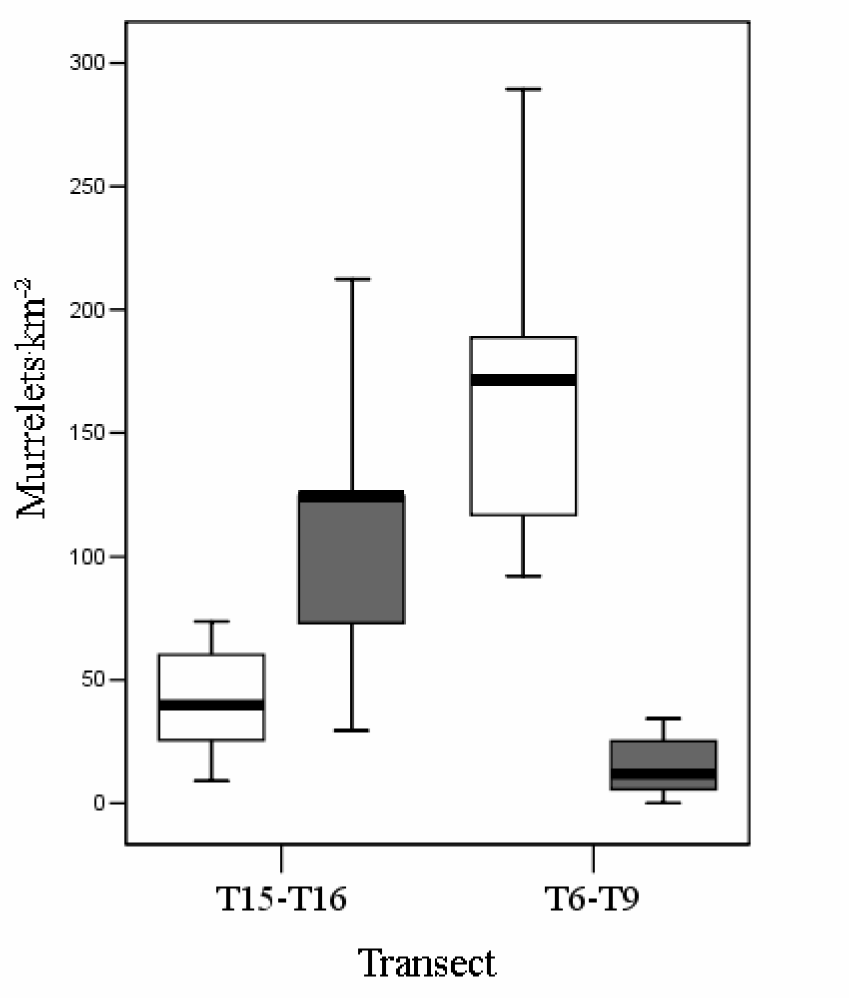

Figure 3. Day (open) and night (closed) densities of murrelets for T6-T9 and T15-T16. The upper and lower quartiles are represented by the boxes, the median by the line separating the upper and lower quartiles and the whiskers represent the minimum and maximum values.

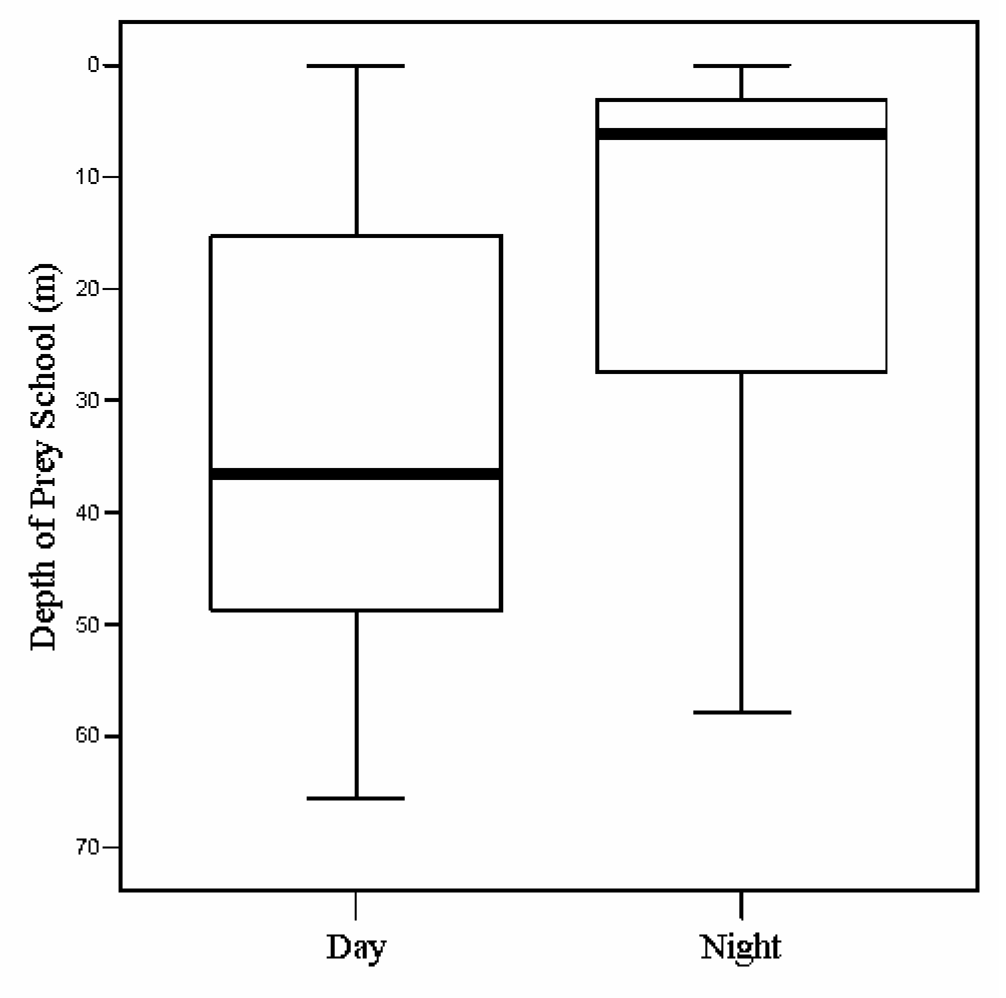

Figure 4. Comparison of depth of prey schools (surface = 0 m) recorded on the echosounder between day (N = 193) and night (N = 50). The upper and lower quartiles are represented by the boxes, the median by the line separating the upper and lower quartiles and the whiskers represent the minimum and maximum values.

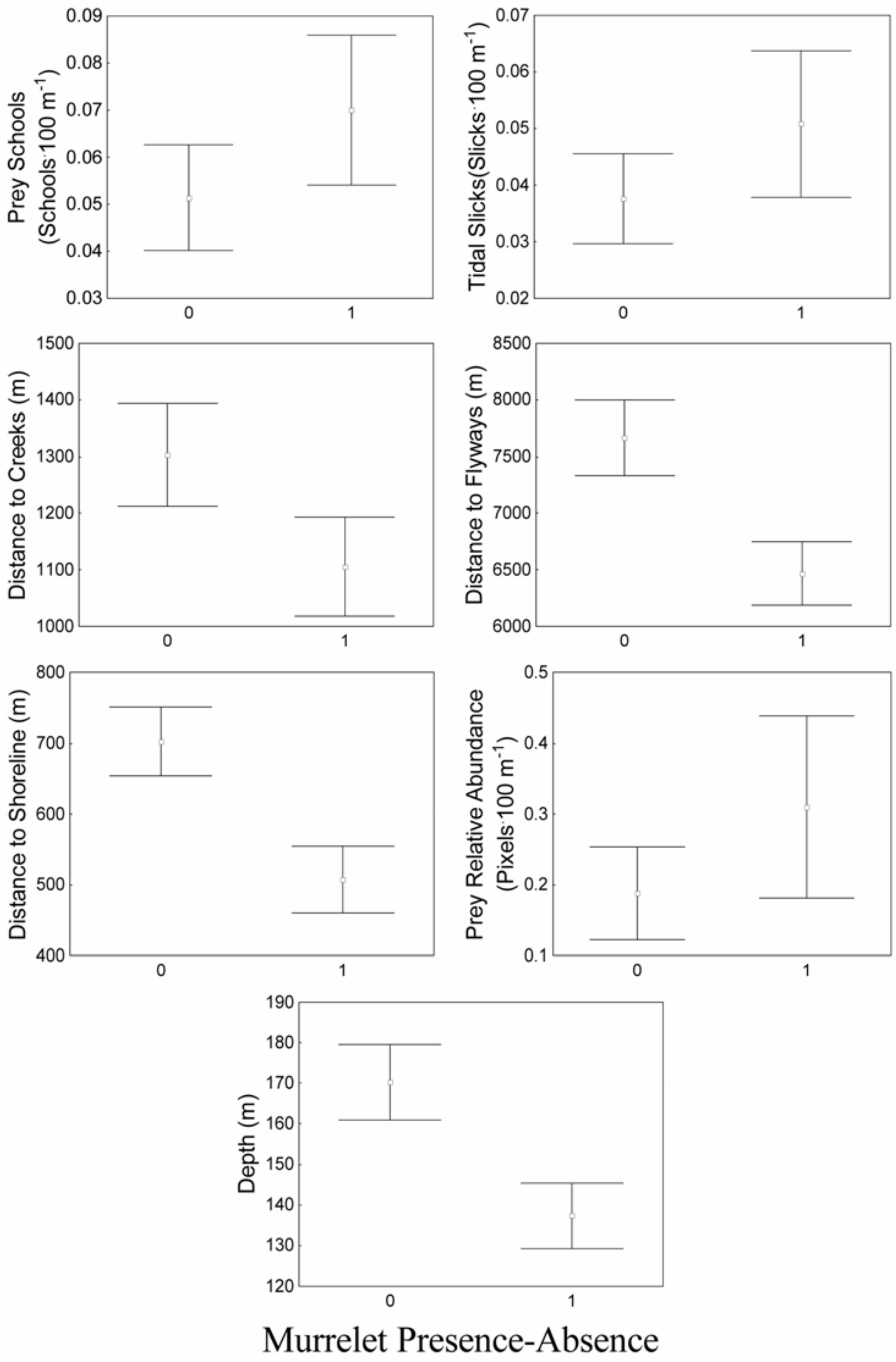

Figure 5. Mean plots for continuous habitat variables grouped by murrelet presence-absence (1-0, respectively). Squares mark mean values and whiskers represent 95% confidence intervals.

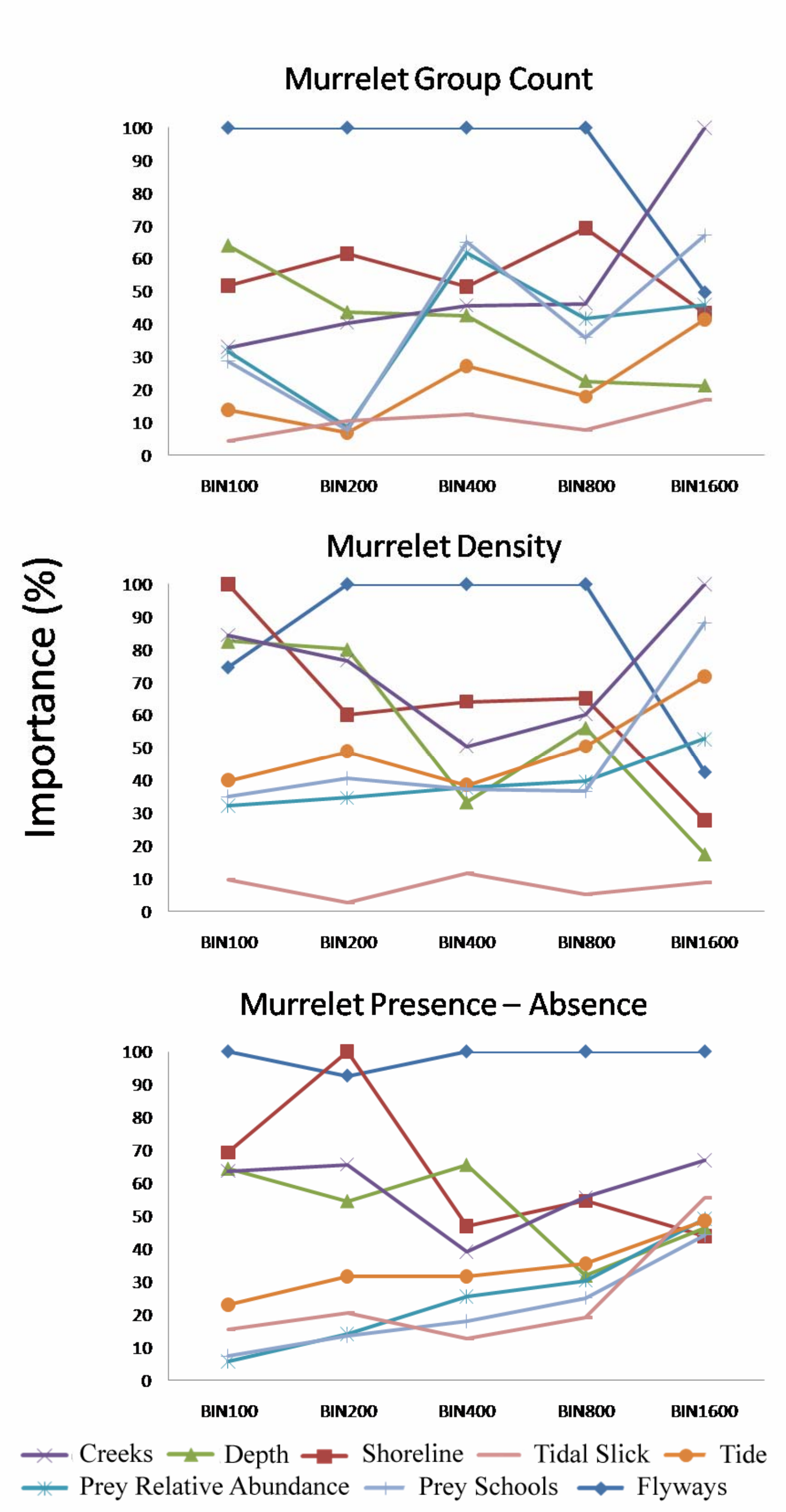

Figure 6. Normalized importance values of the eight independent variables based on ten trees grown for each bin size (100, 200, 400, 800, 1600 m) and each dependent variable (murrelet density, group count and presence-absence) for T1-T16 surveys.

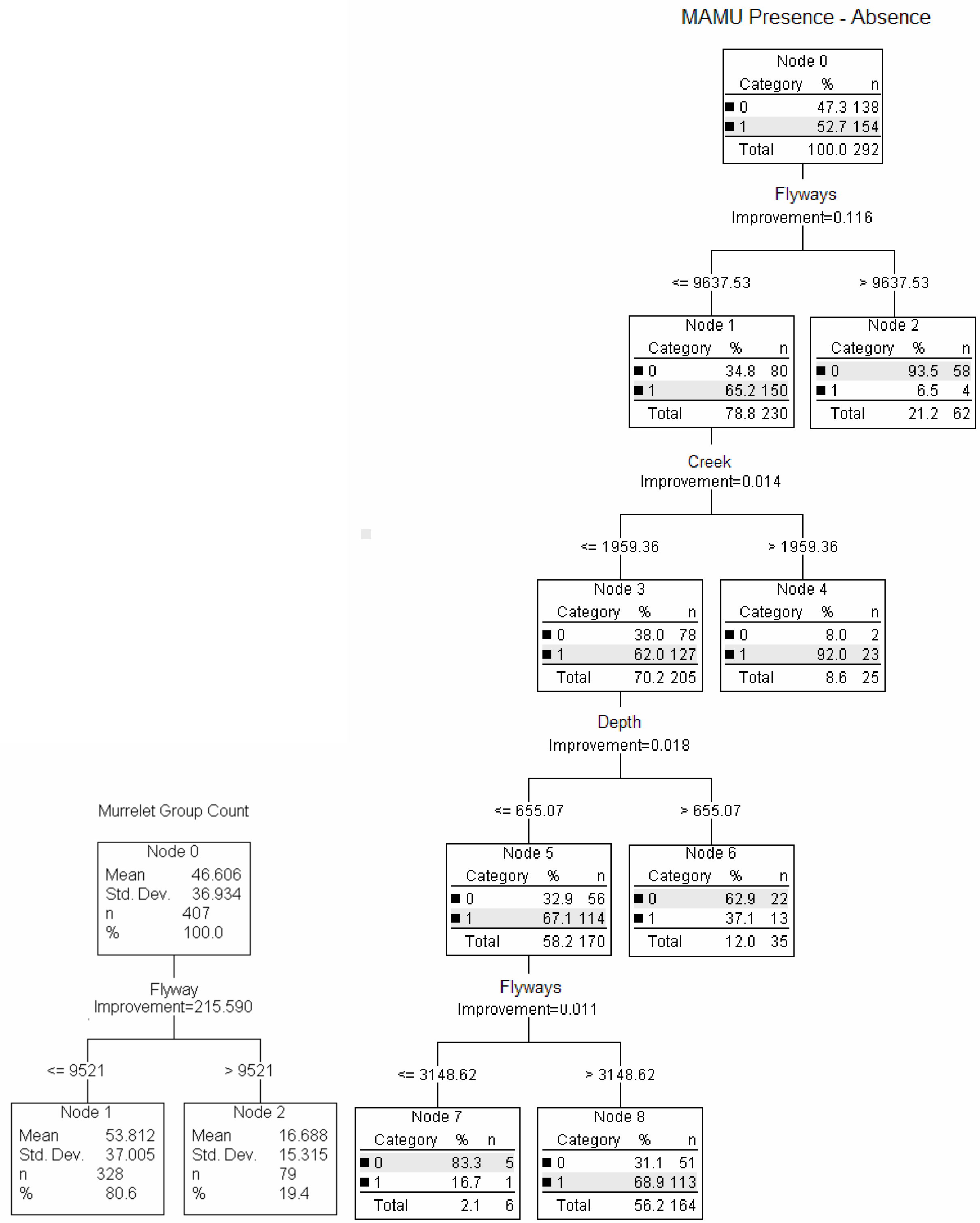

Figure 7. Regression tree for Marbled Murrelet group count(groups·km^{-2}) and presence-absence at the 100 m scale based on seven independent variables: prey schools (schools·km^{-1}), prey relative abundance (pixels·km^{-1}), tidal slick (tidal slicks·km^{-1}), distance to creeks (m), distance to shore (m), distance to flyway (m), and depth (m).

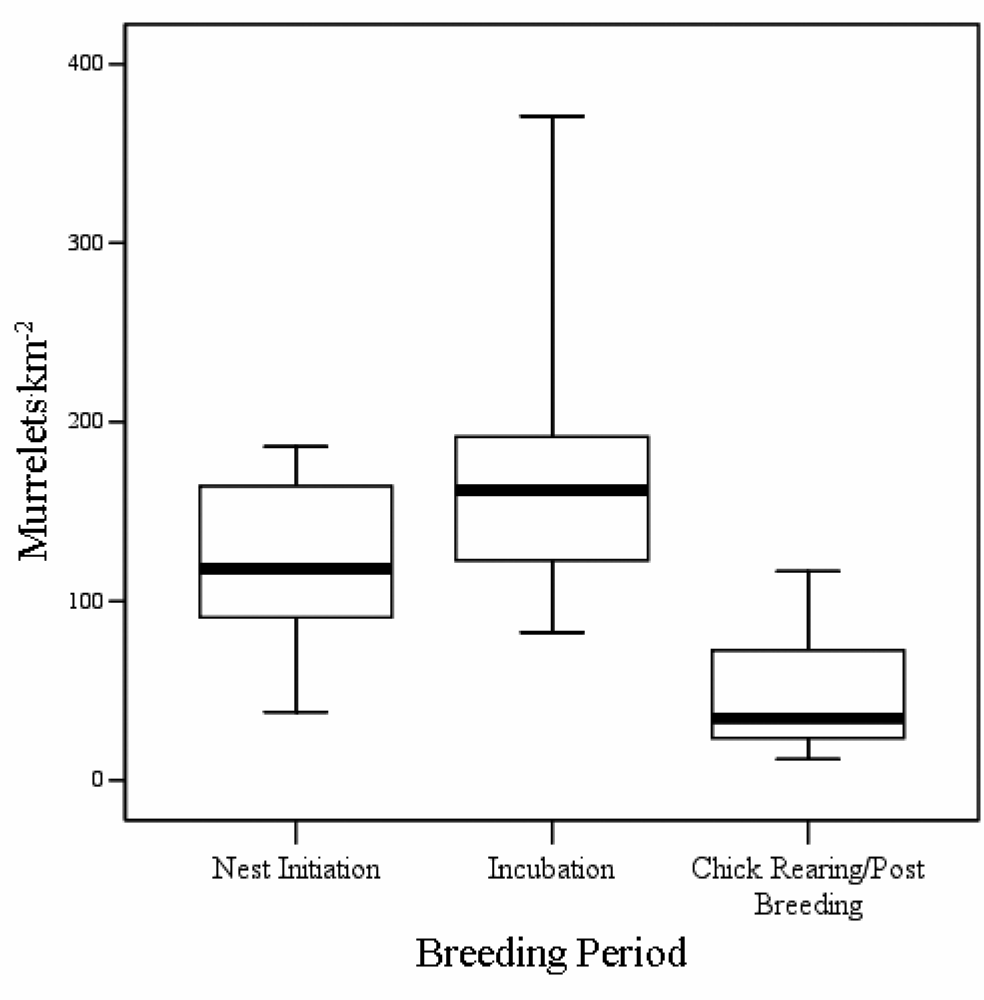

Figure 8. Boxplot of murrelet density *versus* breeding period. Breeding season was broken into three breeding periods: (1) Nesting initiation (25-May to 19-June), (2) Incubation (19-June to 12-July), and (3) chick rearing and post breeding (13 to 27-July). The upper and lower quartiles are represented by the boxes, the median by the line separating the upper and lower quartiles and the whiskers represent the minimum and maximum values.

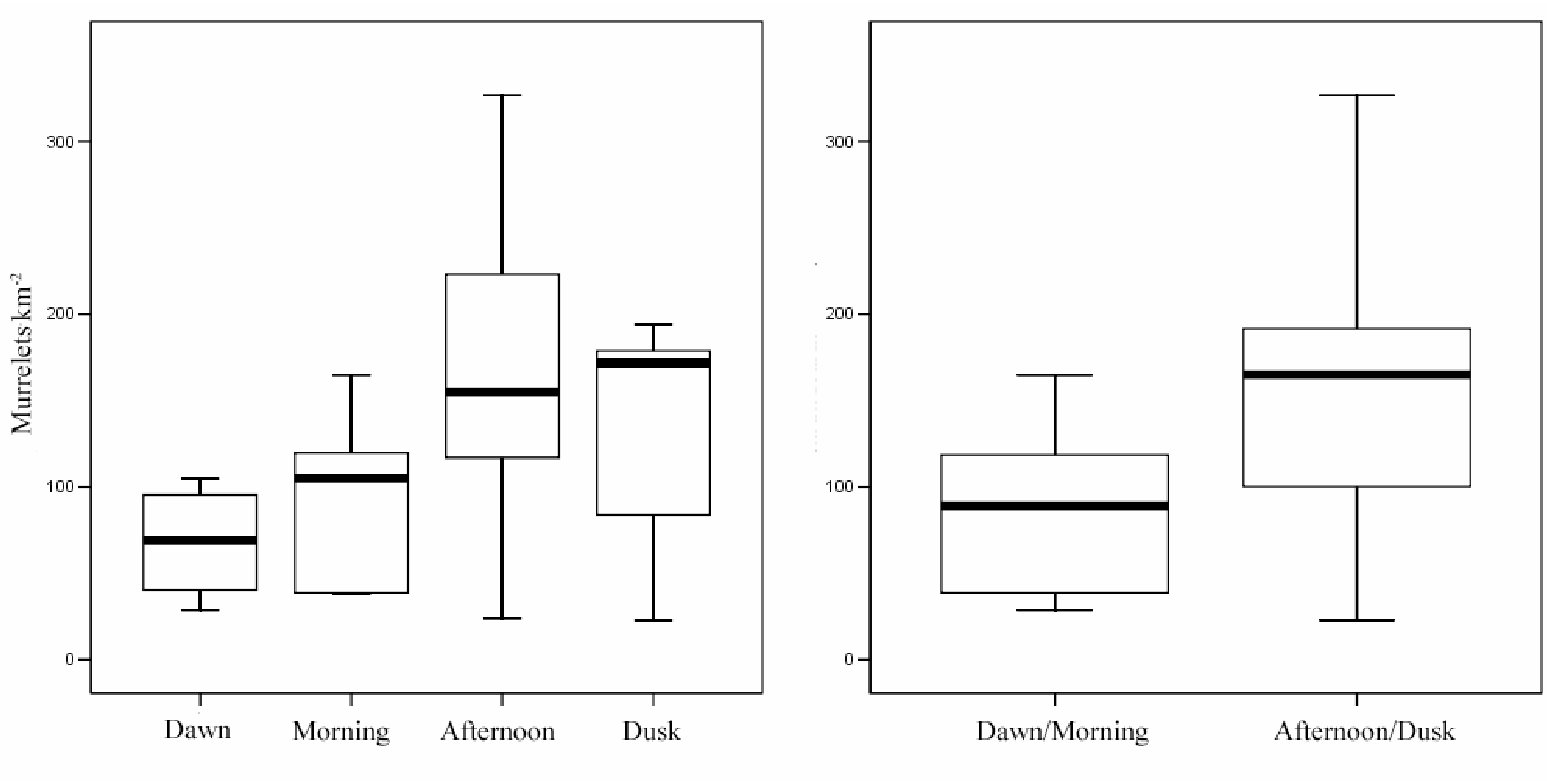

Figure 9. Boxplot of murrelet density for T6-T9 broken into time periods. The upper and lower quartiles are represented by the boxes, the median by the line separating the upper and lower quartiles and the whiskers represent the minimum and maximum values.

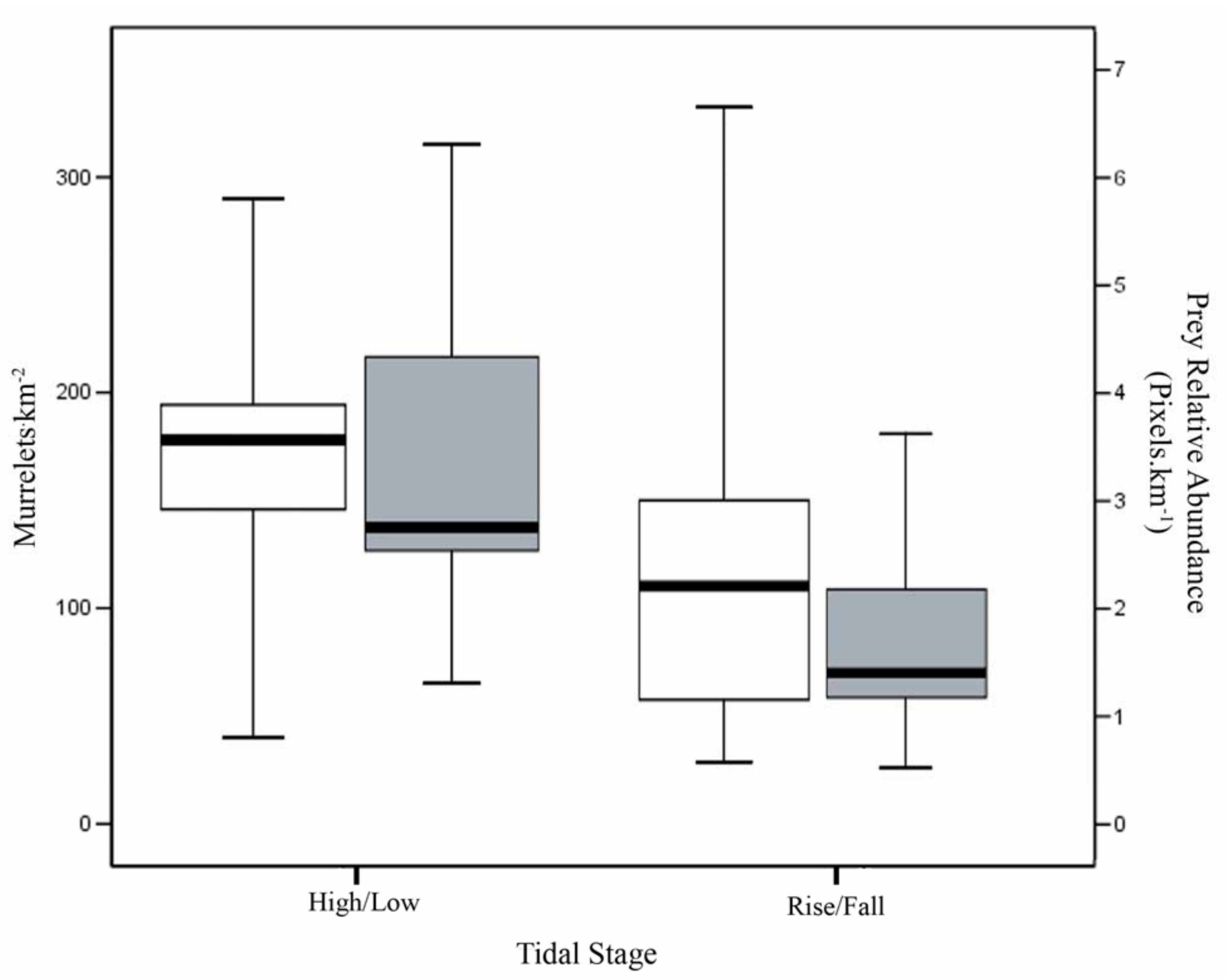

Figure 10. Boxplot of both murrelet density (open boxes) and prey relative abundance (closed boxes) *versus* tidal stage (for T6-T9). Slack tide represents the period one h before and after high or low tide and rise/fall represents all other tide periods. The upper and lower quartiles are represented by the boxes, the median by the line separating the upper and lower quartiles and the whiskers represent the minimum and maximum values.

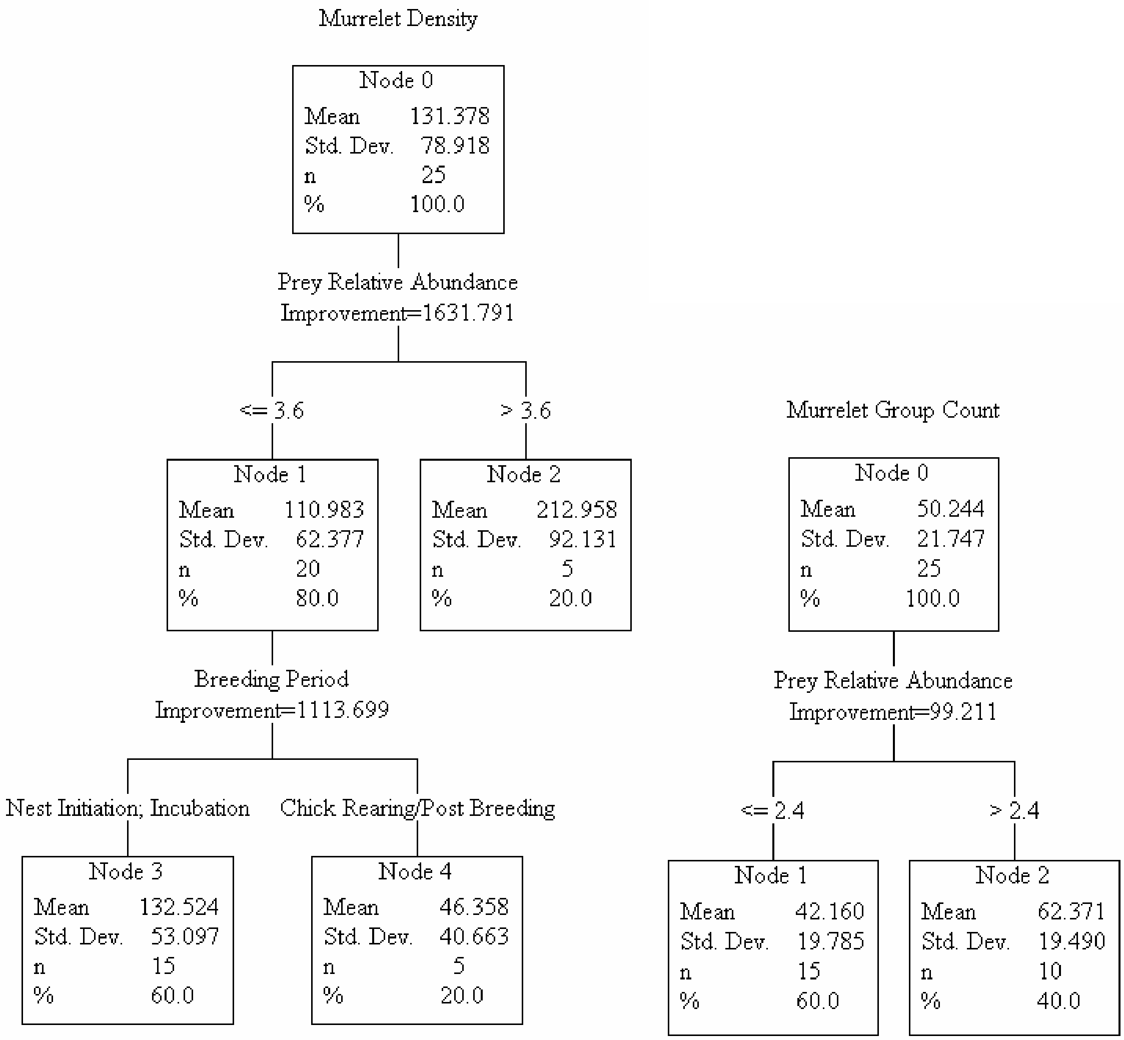

Figure 11. Regression trees for murrelet density (murrelets·km^{-2}) and murrelet group count (groups·km^{-2}) for the T6-T9 region (14.4 km, N = 25) based on six independent variables: prey relative abundance, prey schools, breeding period, tidal slicks, tidal stage, and time of day.

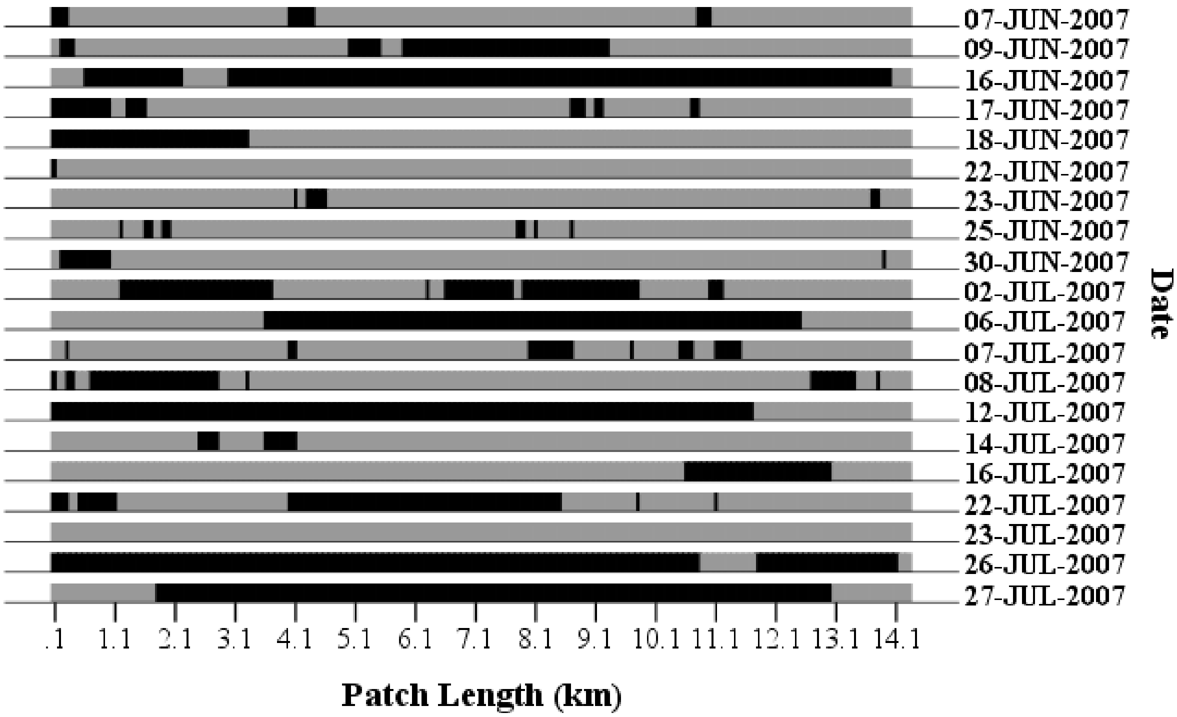

Figure 12. Plot of significant aggregations between murrelets and prey for each study day. Black bars show range of significant aggregation and grey bars show ranges where no significant aggregation exists, based on 99% confidence interval from Monte-Carlo simulation for the Ripley's K analysis.

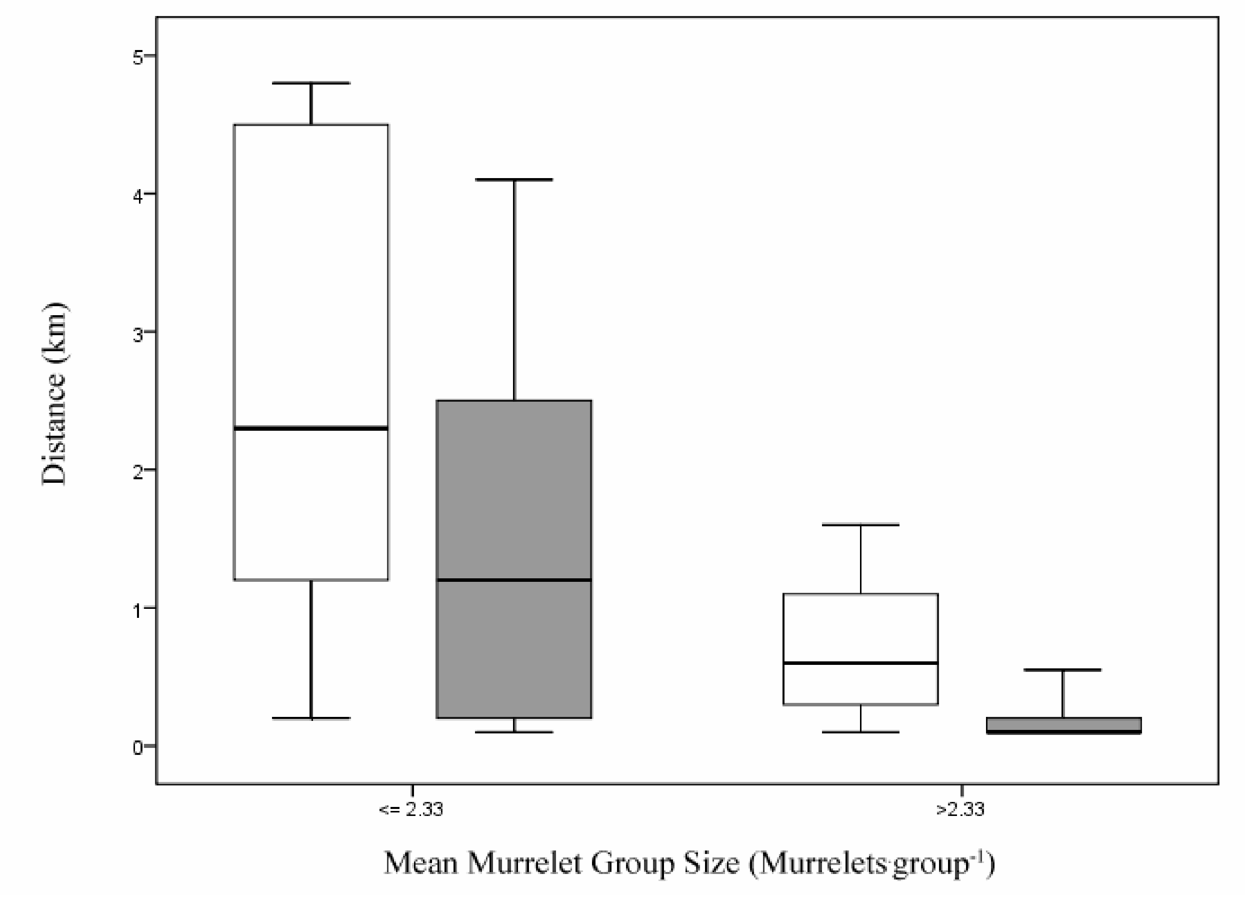

Figure 13. Boxplot of patch length (open boxes) and minimum scale of aggregation (closed boxes) grouped by mean murrelet group size. The upper and lower quartiles are represented by the boxes, the median by the line separating the upper and lower quartiles and the whiskers represent the minimum and maximum values.

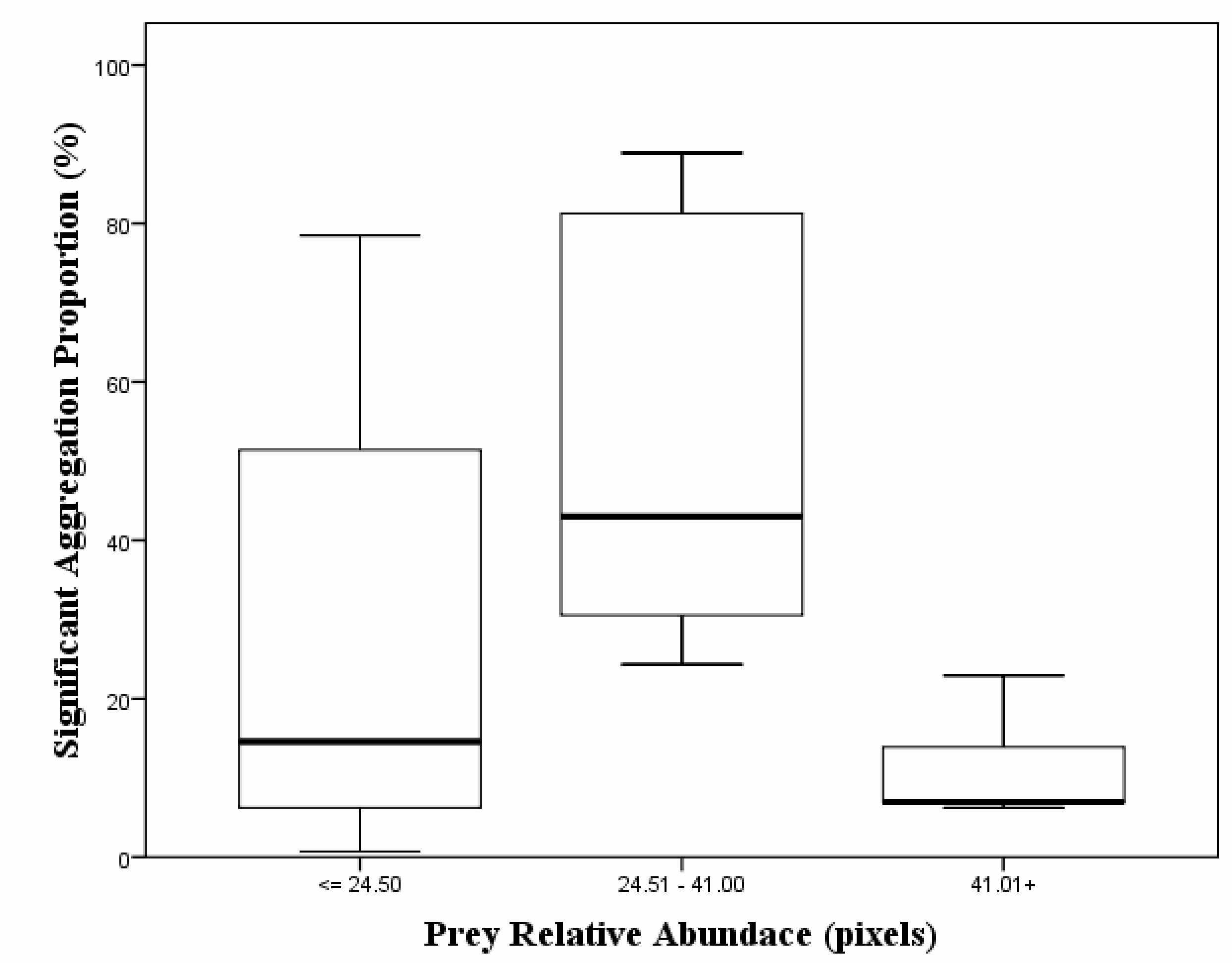

Figure 14. Boxplot of significant aggregation proportion grouped by prey relative abundance. The upper and lower quartiles are represented by the boxes, the median by the line separating the upper and lower quartiles and the whiskers represent the minimum and maximum values.