SPATIAL DISTRIBUTION AND HABITAT USE OF MARBLED MURRELETS *BRACHYRAMPHUS MARMORATUS* AT SEA IN PORT SNETTISHAM, ALASKA

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SUMMARY

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We examined spatial distribution and habitat use of Marbled Murrelets *Brachyramphus marmoratus* during summer 2007 in Port Snettisham, Alaska. Murrelet habitat use at sea depends on a combination of biotic and abiotic factors, with the importance of those factors dependent on the spatial scale of analysis. We expected that murrelet distribution relative to prey would depend on prey abundance, murrelet breeding stage and murrelet aggregation patterns. We modeled murrelet distribution at fine (100, 200, 400, 800 and 1600 m) and meso (14.4 km) scales using classification and regression tree analysis. At fine scales, we examined murrelet density, number of groups and presence–absence in relation to distance to creek, distance to shoreline, distance to flyway, mean depth, tidal slick count, prey schools, prey relative abundance and tidal stage. At most fine scales, distance to flyways was the most important explanatory variable, with prey variables becoming more important as scale increased. However, models of fine-scale habitat use did not perform well (e.g. the regression tree explained only 9.8% of the variance at the 100 m scale). At the meso scale, we examined murrelet density and number of groups in relation to breeding period, tidal stage, time of day, prey schools, prey relative abundance and tidal slick count. We found that low prey availability was associated with lower densities of murrelets. There was an interaction with breeding period, however; under conditions of low prey availability, murrelets were more abundant during incubation and chick-rearing than during nest initiation and postbreeding, suggesting that murrelets remained close to nesting habitat during periods requiring frequent inland flights. 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 to their prey (bivariate). Murrelets exhibited spatial clustering on all transects, with a patch length (scale of clustering) ranging from 0.3 to 9.0 km. Patch length increased at the end of the breeding season (chick rearing and postbreeding). On days when murrelet mean group size was high (>2.33 murrelets/group), murrelets tracked prey at a finer scale and had lower patch lengths, suggesting larger groups were more closely associated with fish and were closer to other groups of murrelets. Comparing clustering characteristics among three prey-abundance categories (low, medium, high), we found murrelets tracked prey over a broader range of scales at medium prey abundance. Results supported our predictions about the spatial nature of murrelet habitat use and confirmed relationships between murrelet spatial distribution and prey abundance, breeding stage and murrelet clustering.

Key words: *Brachyramphus marmoratus*, Marbled Murrelet, spatial distribution, classification and regression tree, Ripley's *K*, spatial clustering, southeast Alaska, habitat modeling

INTRODUCTION

The environmental and social factors that influence seabird distributions depend on scale (Hunt & Schneider 1987, Swartzman & Hunt 2000), with seabirds likely making spatially hierarchical decisions in selecting habitat (Fauchald *et al.* 2000, Becker & Beissinger 2003). One major influence on seabird distributions is the distribution and availability of prey (Tasker *et al.* 1985). Although one would expect seabirds to show a strong aggregative response to prey availability, this is often not the case, especially at small scales (Woodby 1984, O'Driscoll 1998, Swartzman &

Hunt 2000, Fauchald & Erikstad 2002). At larger scales, seabirds occupy the same general regions as their prey (e.g. Logerwell & Hargreaves 1996), but, as the scale becomes finer, the spatial associations between seabirds and prey become weak or highly variable (Fauchald & Erikstad 2002) and depend 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 (Davoren *et al.* 2002), competition (Burger *et al.* 2008, Ronconi 2008) and spatial predator–prey interactions (see Fauchald 2009 for review) arising from prey tracking modes of the predator (e.g. Fauchald *et al.*

2000) and from prey behavior (e.g. Woodby 1984, Logerwell & Hargreaves 1996, Zamon 2003).

Marbled Murrelets *Brachyramphus marmoratus* (hereafter "murrelets") are small alcids whose biology has received much attention because of the species' conservation status (US Fish and Wildlife Service 1992, McShane *et al.* 2004). Current population is thought to be 300 000–400 000 individuals, with roughly 80% of that total in Alaska (Piatt *et al.* 2007). Annual declines of 2–31% have been estimated in portions of the range (McShane *et al.* 2004, Piatt *et al.* 2007). Because murrelets spend most of their lives at sea, understanding their marine ecology has important implications for 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 & Beissinger 2003, Day *et al.* 2003, Ronconi 2008) and local scales (e.g. Becker & 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 murrelets has been examined over the past two decades, researchers have begun to examine their marine habitat requirements only recently (Ronconi 2008).

Marbled Murrelets are the only alcid species known to nest in old-growth forests in North America (Nelson 1997). At sea, murrelets differ from other piscivorous alcids in having a higher affinity for shallow nearshore habitat (Burger *et al.* 2008, Ronconi 2008). In parts of Alaska, murrelet distribution has been correlated with schools of prey (Ostrand *et al.* 1998), but little is known about the marine habitat distribution and requirements of murrelets in southeast Alaska, the geographic center of their range (Piatt *et al.* 2007). Marine habitats vary spatially—for example, local oceanography determines the dominant midwater forage fish available to marine predators, and may vary greatly within even a small region (e.g. Arimitsu *et al.* 2007). Thus, one would expect regional differences in distribution and habitat use of murrelets at sea.

In this study, we examined marine distribution and habitat use of murrelets in southeast Alaska. First, we used a multi-scale approach to examine fine-scale (0.1–1.6 km) distribution in relation to local habitat characteristics and prey distribution. Second, we used a 14.4 km transect to determine how murrelet distribution is affected by habitat characteristics, stage of breeding, tides and time of day. Third, we used Ripley's *K* statistic (Ripley 1981), a measure of spatial clustering, to examine whether murrelets were clustered relative to one another and to their prey. Murrelet habitat use at sea depends on a combination of biotic and abiotic factors, and the estimated importance of those factors may depend on the spatial scale of analysis. In addition, we expected that murrelet distribution relative to prey should depend on prey abundance, breeding stage and clustering of murrelets relative to one another. Seabirds may show poor spatial concordance with prey at fine scales when prey levels are extremely low or high (Vlietstra 2005); thus, we expected murrelets to be more closely associated with prey when prey levels are intermediate. Spatial associations between seabirds and their prey also vary over time (e.g. Schneider & Piatt 1986, Wright & Begg 1997). We therefore expected concordance between murrelets and prey to vary temporally, including a predictable effect of breeding stage.

METHODS

Study area

Port Snettisham is about 40 km south of Juneau, Alaska (Fig. 1). Surrounded by intact old-growth forest, it is part of a large system of channels with fjord characteristics, has a surface area of about 80 km^2 and is undeveloped except for a few small cabins, a power station and a fish hatchery at the northeastern end of Speel Arm. The oceanography is strongly influenced by freshwater inputs from the Speel and Whiting rivers and from numerous perennial creeks. Strong tidal action mixes this freshwater with saltwater draining into Stevens Passage to the southeast. Port Snettisham is 150 km from the open ocean and is buffered from oceanic circulation by Admiralty and Chichagof islands.

Murrelet at-sea sampling

Survey transects zigzagged between opposite shores based on landmarks that aided in navigation (Fig. 1). We conducted surveys May–July 2007 in seas with a Beaufort index ≤ 3 and visibility > 50 m. We counted seabirds in a fixed-width (100 m) strip transect from
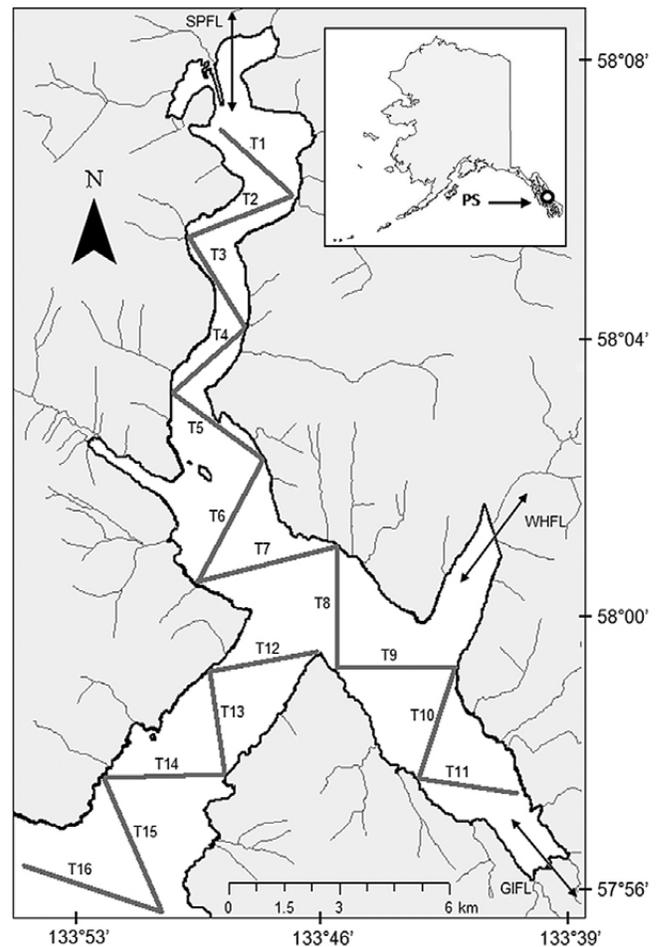

Fig. 1. Transects used to survey the at-sea distribution of Marbled Murrelets in Port Snettisham (PS), Alaska. Gray lines indicate transect route. Double-headed arrows indicate major routes of murrelets flying inland to nesting habitat (GIFL = Gilbert Bay flyway, WHFL = Whiting River flyway, SPFL = Speel River flyway). Numbers on the vertical and horizontal axes are latitude and longitude, respectively.

a 6.1 m aluminum-hull vessel traveling at 14 km/h. Two observers (eye elevation ~2.5 m) used voice recorders to note the observation times and numbers of birds sitting on the water within 50 m on either side of the boat. Birds in flight were not included in the counts. When birds within the strip flushed on approach, observers noted the time when their last location on the water passed perpendicular to the vessel. We towed a buoy 50 m behind the vessel periodically to aid observers in estimating the strip width. Birds within 2 m of each other were considered a group (Becker *et al.* 1997). Observers noted the time when crossing a surface tidal disturbance (hereafter "tidal slick"; Thomson 1981).

A third observer monitored a 200 kHz echosounder (Furuno FCV 585, similar to Burger *et al.* 2004, Huettmann *et al.* 2005, Burger *et al.* 2008, Ronconi and Burger 2008). Using manual settings for range and gain, the echosounder provided continuous information on prey distribution, but we could not identify specific prey types from the echogram. We laid a grid (5 mm × 5 mm) over the screen and set the depth scale to 0–60 m. For each target appearing on the echosounder, the observer recorded time, target depth, bottom depth, target size (relative to grid) and strength. Target strength was scored as strong (with at least a portion of the signal at the highest intensity) or weak (all other targets). We considered only "strong" targets in the analysis, because weak signals appeared to come largely from the halocline or other signal noise. Our analysis also excluded signals from depths below 40 m, where prey would generally be inaccessible to diving murrelets (Burger *et al.* 2004). A global positioning system (GPS) receiver (Garmin 76cs) recorded location every 10 s during the survey. After a survey, birds, tidal slicks and echosounder target data were given waypoints by associating each observation with the GPS location recorded at or near the time of the observation.

We surveyed the study area (T1–T16, Fig. 1) seven times during the season on a biweekly basis and the section T6–T9 an additional 18 times (totaling 25 surveys for the T6–T9 transects). Frequent sampling of T6–T9 provided a larger sample for testing effects of tide, time of day (TOD) and breeding period on murrelet distribution. Low and high tides were defined as peak low or high water ± 1 h. TOD was categorized as: (1) dawn (03h00–06h00), (2) morning (06h00–12h00), (3) afternoon (12h00–19h00) or (4) dusk (19h00–22h00). We divided the breeding season into three periods (Nelson *et al.* 2009): (1) nest initiation (25 May–18 June), (2) incubation (19 June–12 July) and (3) chick rearing and postbreeding (13–27 July).

Statistical analysis

Fine-scale habitat use

We examined murrelet distribution at five linear scales or "bin" sizes (100, 200, 400, 800 and 1600 m) by calculating murrelet density (birds/km^2), group count (groups/km^2), presence–absence and mean values of eight habitat variables for all bins at each scale. Spatial analyses were done in ArcGIS 9.2.

Murrelets used three main flyways for traveling inland: Speel River, Whiting River and Gilbert Bay (Nelson *et al.* 2009, Fig. 1). Murrelet density and group count were analyzed in relation to distance to flyway, distance to nearest creek, distance to shoreline, mean depth, tidal slick count, prey occurrence (schools/km), prey relative abundance (pixels/km) and tidal stage. Distance to a creek,

shoreline or flyway was measured from bin centroid to the feature. We calculated depth for a transect from echosounder 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 was the number of visible disturbances in the water created by tidal currents or upwelling within the bin. Prey occurrence was the number of fish schools detected by the echosounder per kilometer, and prey relative abundance. was the sum of pixels (grid cells on the screen overlay) per kilometer containing strong target signals. Tidal stage for a bin was recorded as rising, high, falling or low (as described above) at the time the bin was surveyed.

Univariate analysis — We quantified univariate relations between pairs of continuous variables at the 100 m scale with Spearman's correlation coefficients (r_s) and relationships between murrelet presence–absence and independent variables with Mann–Whitney *U*-tests.

CART analysis — We analyzed murrelet distribution with respect to habitat features using Classification and Regression Tree (CART) methods (SPSS Version 15.0). CART uses constraints rather than correlates to quantify relationships, in contrast to alternative methods such as Generalized Linear Models (O'Connor 2002). Because limiting factors are largely responsible for shaping habitat use, constraint-based models are preferred for characterizing habitat selection and use (Huston 2002). Also, CART deals automatically with nonparametric data, interaction effects, nonlinear predictors and spatial autocorrelation.

We ran preliminary CART analyses, leaving bins unaveraged across dates, to determine the importance of each independent variable (presence–absence, density and group count) to murrelet distribution at the five spatial scales. At each scale, 100 trees were grown for each dependent variable. Each tree subsampled about 250 points randomly from each dataset. With presence–absence data, bivariate CART analysis is sensitive to high proportions of absence values (De'ath & Fabricius 2000). To compensate for deviations from an ideal 50:50 presence–absence ratio, we used a weighted influence variable to account for differences in the ratio at each scale (Ronconi 2008). Trees were grown using the Gini impurity measure, a liberal minimum improvement of 0.00001 and no pruning to induce growth, a maximum tree depth of five, and a minimum of 10 cases in a parent node and five cases in the child node for growth to continue. Importance values for independent variables were calculated as weighted sums across all tree nodes of the improvements an independent variable achieved when 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 of each independent variable averaged across dates (i.e. each bin took one value of each variable based on averages from the seven surveys). Averaging decreases sample size but helps to maintain the spatial independence of points. Tidal stage was not included in the final trees because its values could not be averaged. For presence–absence data, we designated murrelets as "present" in a specific bin if they occurred more often than the mean number of times they occurred in all bins at the same scale. Likewise, "absent" meant murrelets were present in the bin less often than the mean. Trees were built using the same methods as above but with a minimum improvement of 0.001 and pruning to 1 standard deviation (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 segment of the survey (transects T6–T9 combined, Fig. 1) to test for relationships of murrelet density and group count to breeding stage, tidal stage, time of day, prey schools, prey relative abundance and tidal slicks. Sampled 25 times through the season, this segment was appropriate for meso-scale analysis.

Univariate analysis — We examined Spearman's correlation coefficients (r_s) between continuous variables and compared murrelet densities among breeding periods, TOD and tidal stages using Kruskal–Wallis tests. In addition to the four TOD categories defined earlier, we collapsed the categories (dawn–morning being 03h00–12h00 and afternoon–dusk being 12h00–22h00) and compared murrelet density, group count, prey schools and prey relative abundance between periods using Mann–Whitney *U*-tests. Similarly, we compared murrelet density in relation to four tidal stages (as above) and two collapsed categories: (1) slack (low and high tides) and (2) rise–fall (periods of rising or falling tide) with 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, but we used all the data to train the model because of the small sample size.

Spatial scale of clustering

Ripley's *K* statistic (Ripley 1981) tests whether spatial distributions depart from random, being either clustered or regularly distributed (Cornulier & Bretagnolle 2006). The *K* statistic can be used to decide whether aggregation exists and at what spatial scales. Because our sample frame was long and narrow (several kilometers by 100 m wide), we treated the data as one-dimensional to avoid large edge effects. Thus, distance between birds was given by the path traveled on the transects rather than the actual two-dimensional

distances. Details of the *K* statistic and its use are available in Ripley (1981), O'Driscoll (1998), Burger *et al.* (2004) and Wiegand & Moloney (2004).

Univariate — We calculated Ripley's *K* for all transects (T1–T11, T6–T9, T12–T16) in MatLab (R2007B) using routines developed by O'Driscoll (1998), and we compared patch length and crowding values among the three count types with Kruskal–Wallis tests. We compared patch length and crowding among breeding periods using a Kruskal–Wallis test for transects T6–T9. Values deviating more than two standard deviations were treated as outliers and removed from the analysis. We divided densities into three categories of equal size—low <1.47, medium 1.47–2.73 and high >2.73 for prey relative abundance (pixels/km) and low <0.56, medium 0.56–0.70 and high >0.70 for prey schools (schools/km)—and used a Kruskal–Wallis statistic to test for differences in crowding and patch length in each dependent variable.

"Crowding" is a measure of aggregation intensity (mean number of murrelets in a patch exceeding the expected number when compared to a random distribution) at a given scale, whereas "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 small fluctuations influencing the patch length, we defined the patch length as the scale at which aggregation was higher than the next three successive values, following O'Driscoll *et al.* (2000).

Bivariate — We ran a bivariate analysis of murrelet distribution in relation to prey for T6–T9 (n = 20), also following O'Driscoll (1998). For each survey, we examined four parameters that describe how murrelets track prey: (1) minimum scale of aggregation, (2) patch length, (3) crowding and (4) significant aggregation proportion. Minimum scale of aggregation was the smallest scale at which aggregation was higher than the 99% confidence interval obtained from a Monte-Carlo randomization. Patch length and crowding were defined as above, and significant aggregation proportion was

TABLE 1
Bivariate Spearman's correlation (r_s) of continuous dependent and independent variables[a]

Variable	Murrelet density	Murrelet group count	Prey schools	Prey relative abundance	Tidal slick	Distance to creek	Distance to flyways	Distance to shoreline
Murrelet group count	0.898 $P<0.01$							
Prey schools	0.140 $P<0.01$	0.155 $P<0.01$						
Prey relative abundance	0.141 $P<0.01$	0.156 $P<0.01$	0.979 $P<0.01$					
Tidal slick	0.018	0.048	-0.008	-0.012				
Distance to creek	-0.118 $P<0.01$	-0.190 $P<0.01$	-0.096 $P<0.05$	-0.095 $P<0.05$	0.019			
Distance to flyways	-0.222 $P<0.01$	-0.259 $P<0.01$	-0.216 $P<0.01$	-0.197 $P<0.01$	-0.182 $P<0.01$	0.217 $P<0.01$		
Distance to shoreline	-0.178 $P<0.01$	-0.292 $P<0.01$	-0.178 $P<0.01$	-0.179 $P<0.01$	0.013	0.655 $P<0.01$	0.237 $P<0.01$	
Depth	-0.255 $P<0.01$	-0.275 $P<0.01$	-0.061	-0.053	-0.028	0.249 $P<0.01$	0.285 $P<0.01$	0.150 $P<0.01$

[a] No adjustment of significance values for multiple comparisons. *P* values from two-tailed tests.

defined as the proportion of total transect length (14.4 km, divided into 100 m intervals) that had significant aggregation. As such, significant aggregation proportion represents the range of scales at which murrelets tracked prey.

We compared the four descriptors of spatial distribution above to six independent variables: murrelet density (low or high, cut value = 142 murrelets/km), group count (low or high, cut value = 58 groups/km), prey schools (low, medium or high, cut values = 0.56 and 0.70 schools/km), prey relative abundance (low, medium or high, cut values = 1.47 and 2.73 pixels/km), mean murrelet group size (murrelet count divided by number of groups, low or high, cut value = 2.33 murrelets/group) and stage of breeding (as above). Cut values were the 50th (low–high) or 33rd and 66th (low–medium– high) percentiles. We examined three levels of prey relative abundance and prey schools to see whether maximum response occurred at medium values, as suggested by Vlietstra (2005). As data were not normally distributed, we used a Kruskal–Wallis test of differences among multiple groups and a Mann–Whitney test for two groups. If the Kruskal–Wallis test was significant, a *post hoc* Mann–Whitney test identified pair-wise differences. Throughout our analyses, we used $P = 0.05$ to determine statistical significance.

RESULTS

We counted 8890 birds on the transects, with murrelets making up 93% of the total (mean ± SD = 111 ± 35 and 130 ± 77 murrelets/km² for T1–T16 and T6–T9, respectively). Murrelets were predominantly found in singles (34%) and pairs (42% of all sightings).

Fine-scale habitat use

Univariate analysis — At the 100 m bin scale, both murrelet density and group count were negatively correlated with depth and with distances to shoreline, creeks and flyways (Table 1). Prey variables were also negatively correlated with distances to

shoreline, creeks and flyways. Murrelet presence–absence showed similar relationships—prey schools, prey relative abundance, depth and distances to shoreline, creeks and flyways all were significantly correlated with murrelet presence–absence, but tidal slicks were not (Table 2).

CART analysis — For each dependent variable, distance to flyways was the best explanatory variable at almost every scale (Fig. 2). Distance to creeks was also important at most scales for all three dependent variables and was the most important variable for murrelet density and group count at the 1600 m scale. For murrelet presence–absence, however, distance to creeks showed a decreasing importance with increasing bin size. Depth was important at small bin sizes (e.g. second in importance at the 100 m bin size for all three dependent variables) but decreased as bin size increased. Tidal stage, tidal slicks, prey schools and prey relative abundance became more important as bin size increased.

The final tree for murrelet density at the 100 m bin scale produced no nodes and therefore did not grow. The trees for murrelet group count and presence–absence each grew two nodes (Fig. 3). For both trees, the split was based on a distance to flyways approximating 9.6 km; that is, there were more murrelet groups and their density was higher within 9.6 km of the major flyways. At the 100 m bin scale, the regression tree built for murrelet group count performed poorly, explaining only 9.3% of the variance. The classification tree had a 68.6% classification rate based on the test sample. Because the data used to build the model had a presence–absence ratio of about 50:50, the tree improved classification by roughly 19 percentage points over a null model allocating bins randomly to "murrelets present" or "murrelets absent."

Meso-scale habitat use

Univariate analysis — We found no significant correlations between independent and dependent continuous variables other

TABLE 2
Mann–Whitney U tests at the 100 m scale using murrelet presence–absence as the grouping variable

Variable	Murrelet presence–absence	Mean ± SD	U	Adjusted Z	P
Prey schools (schools/100 m)	Present	0.070 ± 0.112	15566	-2.705	0.007
	Absent	0.044 ± 0.095			
Prey relative abundance (pixels/100 m)	Present	0.310 ± 0.112	15501	-2.791	0.005
	Absent	0.172 ± 0.696			
Tidal slicks (slicks/100 m)	Present	0.508 ± 0.910	16419	-1.78	0.075
	Absent	0.344 ± 0.716			
Distance to creeks (m)	Present	1105 ± 617	14393	3.254	0.001
	Absent	1408 ± 854			
Distance to flyways (m)	Present	6467 ± 1976	11814	5.683	<0.001
	Absent	8242 ± 3145			
Distance to shoreline (m)	Present	508 ± 335	12365	5.164	<0.001
	Absent	760 ± 472			
Depth (m)	Present	451 ± 186	12246	5.276	<0.001
	Absent	559 ± 209			

than the expected correlations between murrelet density and group count ($r_s = 0.891$, $P < 0.01$), and prey relative abundance and prey schools ($r_s = 0.600$, $P < 0.01$). Mean murrelet density differed among breeding periods (Kruskal–Wallis, n = 23, $H = 9.765$, $P = 0.008$), and post-hoc comparisons showed that chick rearing and postbreeding period had significantly lower counts than incubation period ($Z = 3.1192$, $P = 0.005$).
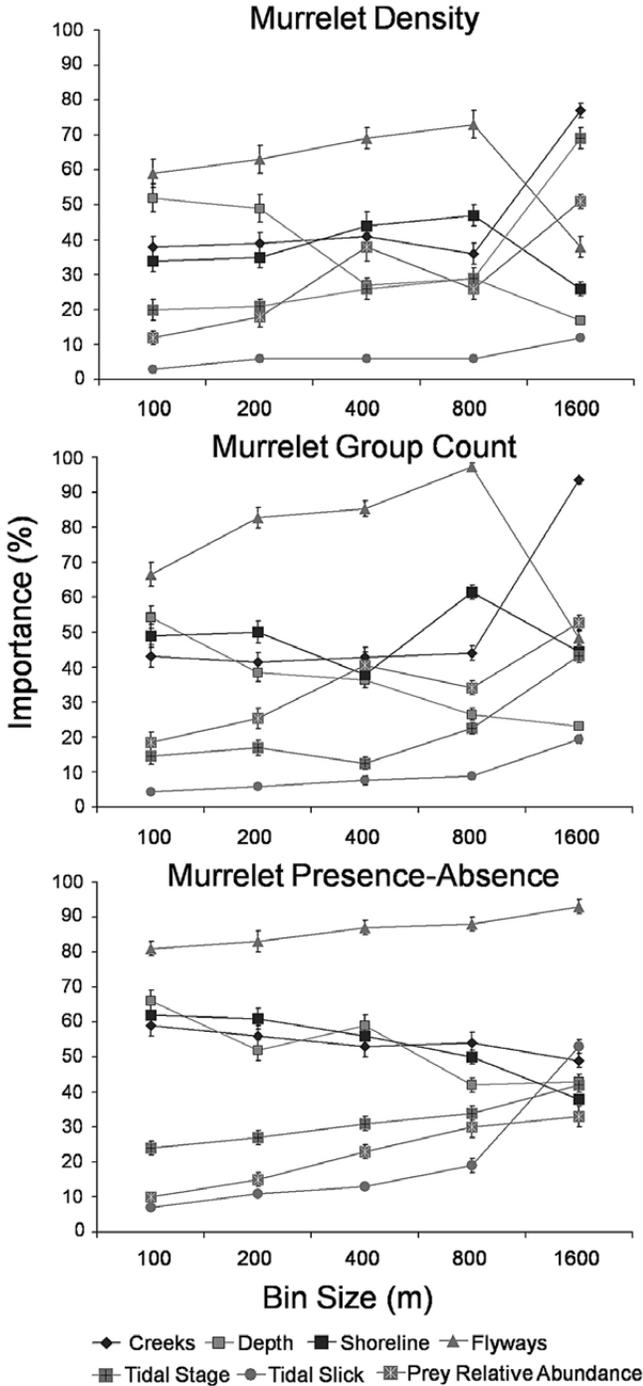
No difference in murrelet densities existed among four TOD categories ($\chi^2 = 4.9$, $P = 0.108$), but when TOD was grouped into two categories, murrelet density was higher during afternoon–dusk than during dawn–morning ($Z = -2.195$, $P = 0.028$; Fig. 4). No significant relationships were detected between dawn–morning and afternoon–dusk for prey schools ($U = 38.5$, $Z = -0.7329$, $P = 0.473$) or prey relative abundance ($U = 41.0$, $Z = -0.5401$, $P = 0.624$).

Overall, we found a difference in murrelet density among tide heights (Kruskal–Wallis, $H = 8.647$, n = 45, $P = 0.034$), but no pairwise comparison was significant. Grouping tidal stages into slack (high–low) and rise–fall categories, we found a higher density of murrelets ($U = 28.0$, $Z = -2.0656$, $P = 0.040$) and greater
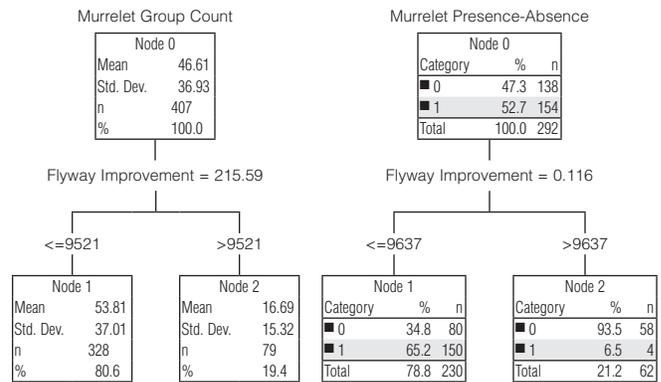

Fig. 3. Regression tree for Marbled Murrelet group count (groups/km²) and presence–absence at the 100 m scale based on seven independent variables: prey schools (schools/km), prey relative abundance (pixels/km), tidal slick (tidal slicks/km), distance to creeks (m), distance to shore (m), distance to flyway (m) and depth (m).
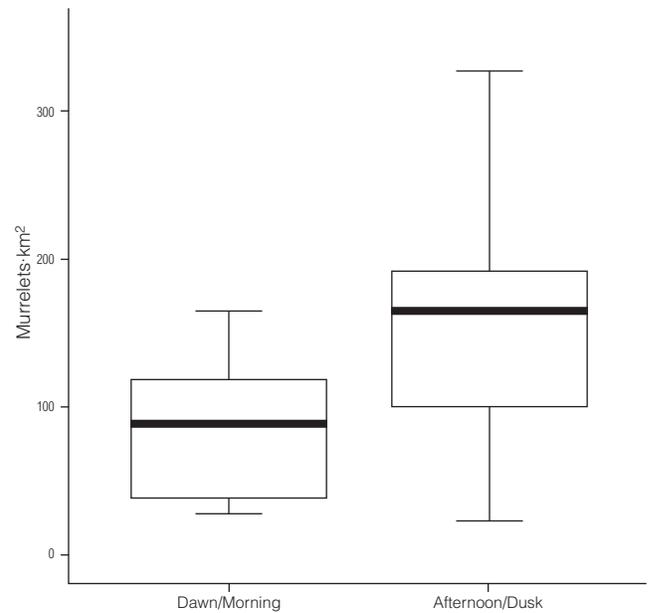

Fig. 2. Mean normalized importance values (T1–T16 surveys) of the eight independent variables for each dependent variable (murrelet density, group count and presence–absence) based on 100 trees grown for each bin size (100, 200, 400, 800, 1600 m). Prey schools (not included in the figure) showed a similar pattern in importance to prey relative abundance. Error bars are standard errors.

Fig. 4. Boxplot of murrelet density for T6–T9, broken into time periods. Murrelet density was significantly higher during afternoon–dusk than during dawn–morning ($Z = -2.195$, $P = 0.028$). Upper and lower quartiles are represented by the boxes, the median by the line separating the upper and lower quartiles; whiskers are minimum and maximum values.

prey relative abundance ($U = 5.0$, $Z = -3.2203$, $P = 0.001$) during slack tides (Fig. 5). We found no significant relationship between prey schools and the grouped tidal stages ($U = 27.5$, $Z = -1.3660$, $P = 0.177$).
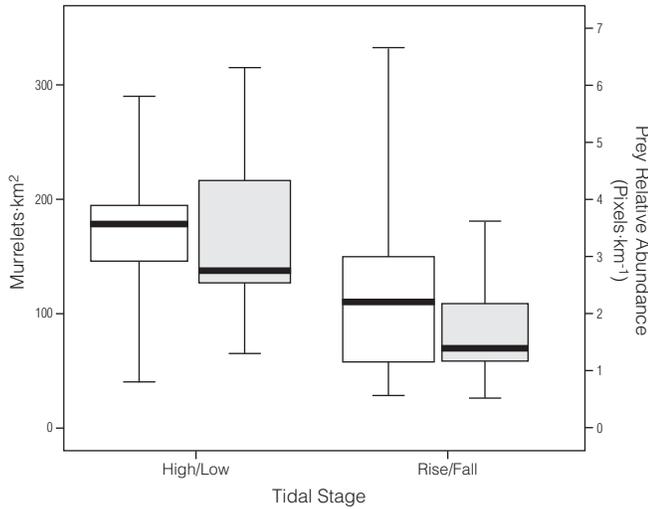

Fig. 5. Boxplots of murrelet density (open boxes) and prey relative abundance (shaded boxes) versus tidal stage (for T6–T9). Slack tide was the period 1 h before and after high or low tide; rise/fall represents all other tide periods. Higher murrelet density ($U = 28.0$, $Z = -2.0656$, $P = 0.040$) and prey relative abundance ($U = 5.0$, $Z = -3.2203$, $P = 0.001$) occurred during slack tides. Upper and lower quartiles are represented by the boxes, the median by the line separating the upper and lower quartiles; whiskers are minimum and maximum values.
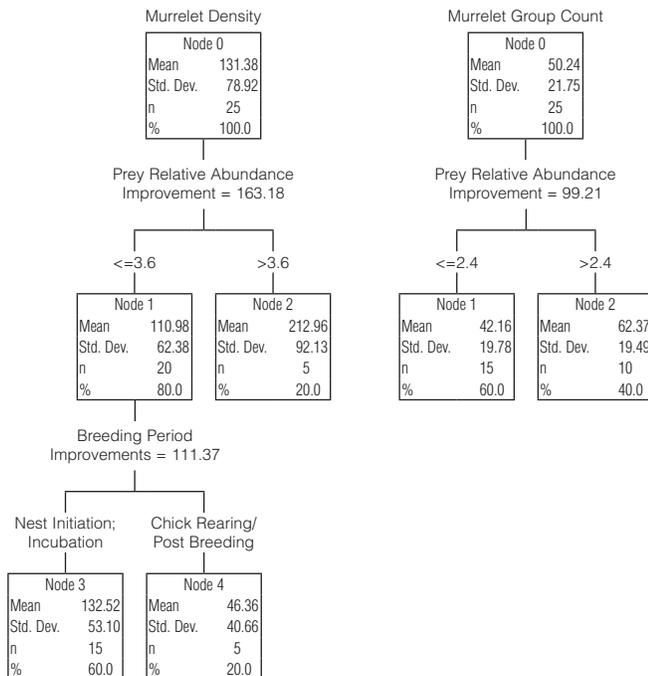
CART analysis — Murrelet density and group count trees branched initially on prey relative abundance, murrelets being more abundant and in larger groups on transects where prey relative abundance was high (Fig. 6). Murrelet density at high prey relative abundance (210 birds/km^2) was almost twice that at low prey relative abundance (110 birds/km^2). Although both trees were split on similar values of the same variable, the improvement to the murrelet density tree was much larger than the improvement to the tree for group count. The murrelet density tree was further split on breeding period, which also gave a relatively large improvement. Murrelet densities in T6–T9 were higher during nest initiation and incubation than during chick rearing and postbreeding. The tree for murrelet density performed best, explaining 48.9% of the variance in the training dataset, whereas the regression tree for murrelet group count explained 24.5% of the variance.

Spatial scale of clustering

Univariate — All transects showed significant clustering in the distribution of murrelets (Table 3). The three abundance measures had slight, nonsignificant differences in patch length and crowding (patch length $\chi^2 = 4.06$, $P = 0.131$; crowding $\chi^2 = 4.02$, $P = 0.134$).

Crowding was similar among breeding stages (Kruskal–Wallis, $H = 2.214$, $P = 0.331$), but patch length differed significantly (Kruskal–Wallis, $H = 7.229$, $P = 0.027$). Pairwise comparisons showed that patch length was larger during chick rearing and postbreeding than it was during nest initiation ($Z = 2.684$, $P = 0.007$) and incubation ($Z = 2.052$, $P = 0.040$).

TABLE 3
Patch length and crowding values from the Ripley's *K* analysis of murrelet spatial distribution

Transect	n	Patch length (km)		Crowding (birds/patch)	
		Mean ± SD	Range	Mean ± SD	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

Fig. 6. Regression trees for murrelet density (murrelets/km^2) and murrelet group count (groups/km^2) for the T6–T9 transects (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.
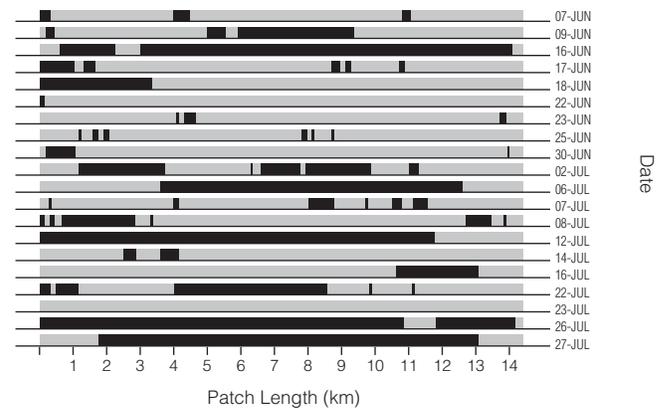

Fig. 7. Plot of significant aggregations between murrelets and prey for each day of the study. Black bars show ranges of significant aggregation; gray bars show ranges where no significant aggregation occurred, based on a 99% confidence interval from Monte-Carlo randomizations of the data before Ripley's *K* analysis.

Prey schools (mean 0.69 [SD 0.33] schools/km) yielded no differences in crowding (Kruskal–Wallis; $H = 0.599$, $P = 0.741$) or patch length (Kruskal–Wallis; $H = 0.283$, $P = 0.868$) among high, medium and low categories. Prey relative abundance (mean 2.99 [SD 2.85] pixels/km) likewise yielded no differences in crowding ($n = 19$, $H = 0.942$, $P = 0.624$) or patch length ($n = 19$, $H = 0.642$, $P = 0.725$).

Bivariate — Murrelets showed significant aggregation relative to prey on 19 of the 20 surveys, but the scales of aggregation differed dramatically among days (Fig. 7). Days with high mean group size (> 2.33 murrelets) had a lower minimum significant scale (smallest scale at which murrelets tracked prey) compared with days when group size was one to two birds (Table 4). Larger group size was also associated with shorter patch length (Table 4). Finally, significant aggregation proportion differed among three categories of prey relative abundance (Table 4), with medium prey abundance yielding a higher significant aggregation proportion than either low ($n = 12$, $U = 4.0$, $P = 0.028$) or high ($n = 13$, $U = 7.0$, $P = 0.045$) prey abundance. Low and high values did not differ significantly from each other ($n = 11$, $U = 12.0$, $P = 0.058$).

DISCUSSION

Top predators rarely occur in high densities in the marine environment, but when they do they may exert top-down effects on the ecosystem at a regional scale (Hunt & McKinnell 2006). In Port Snettisham, murrelets occurred at higher densities than studies of other areas have found, suggesting this area is important for murrelets. For example, our study area (T1–T16) had a mean density of 111 (SD 35) murrelets/km^2, whereas Agler *et al.* (1998) found an overall mean density of *Brachyramphus* murrelets (Marbled and Kittlitz's *B. brevirostris* murrelets) in southeast Alaska of 19.4 birds/km^2, but also found areas with densities >150 birds/km^2. 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 45.26 (SD 10.1) murrelets/km^2. Given that murrelets are the numerically dominant seabird in the Port Snettisham region, they likely play an important role in ecosystem function as a top marine predator, affecting local prey distribution and abundance.

TABLE 4
Statistical tests (Mann–Whitney between two groups, Kruskal–Wallis among three groups)
for all four aggregation parameters and six independent variables[a]

Parameter	Statistic	Minimum scale of aggregation (km)	Patch length (km)	Crowding (birds/patch)	Significant aggregation proportion (km)[b]
Range		0.1–4.1	0.1–4.8	0.86–88.80	0–13.2
Mean		0.92	1.58	15.08	4.63
SD		1.27	1.58	20.96	4.52
Murrelet density	*U*	19	21	33	31.5
	Z	-1.73	-1.445	-0.289	-0.795
	P	0.084	0.148	0.773	0.427
Murrelet group count	*U*	29.5	31.5	28	38.5
	Z	-0.281	-0.434	-0.77	-0.177
	P	0.779	0.665	0.441	0.86
Mean murrelet group size	*U*	**11.5**	**14.5**	35	35.5
	Z	**-2.493**	**-2.298**	-0.096	-0.442
	P	**0.013**	**0.022**	0.923	0.659
Prey schools	*U*	25.5	25.5	31	37
	Z	-0.73	-1.012	-0.481	-0.309
	P	0.465	0.213	0.63	0.757
Prey relative abundance	*H*	1.713	2.061	0.493	**9.199**
	P	0.425	0.357	0.781	**0.01**
Breeding periods	*H*	1.713	2.061	0.316	2.125
	P	0.425	0.357	0.854	0.346

[a] Significant results ($P < 0.05$) in bold.
[b] Transect length 14.4 km.

Fine-scale habitat use

Murrelets fly inland to nest sites, often several times each day, depending on the breeding stage. Thus, murrelets congregate in waters adjacent to inland flyways to stage for their inland flights (Nelson 1997). Although CART trees at the 100 m scale did not perform well overall, they showed murrelets were more likely to be found within about 10 km of a flyway (presence–absence), and the number of murrelet groups was also higher within that range. Waters within 9.6 km from one of the major flyways encompassed a large part of the study area. In essence, murrelets were staying mainly within estuarine portions of Port Snettisham and avoiding the area close to Stevens Passage.

Murrelets have been associated with estuarine waters in other regions (Miller *et al.* 2002, Yen *et al.* 2004, Ronconi 2008), possibly because estuaries constitute important foraging habitat for murrelets (Yen *et al.* 2004). In mountainous areas, estuaries are often found at the entrances to major watersheds, which in turn provide flight corridors for murrelets in reaching inland nesting habitat (e.g. Burger 1997). Thus, the relative importance of estuaries as either foraging sites or as staging areas is open to question.

As the scale of our analysis increased to 1600 m, flyways became less important and distance to creeks (followed by prey relative abundance) were better correlated with murrelet density and group count. There may have been some confounding of variables, however. At the 100 m scale, the classification tree indicated birds were more likely to be present at distances greater than 2 km from the nearest creek—the opposite of the finding from the univariate analysis, which showed murrelets were found closer to creeks. Because major flyways were also "creeks," the discrepancy was probably related to the covariance of distance to creeks and distance to flyways.

In two recent studies of murrelet habitat use in British Columbia, Ronconi (2008) and Barrett (2008) found that distance to old-growth forest habitat was an important variable determining marine habitat use during breeding season. Another variable important in both studies was distance to "beach" habitat, possibly because of its association with Pacific Sand Lance *Ammodytes hexapterus* (Haynes *et al.* 2007, 2008b). Old-growth forest is found throughout the Port Snettisham area, but beach habitat is scarce. Sand lance were not encountered in abundance within our study area during prey surveys (Haynes *et al.* 2008a).

Similar to other studies (Logerwell & Hargreaves 1996, Fauchald *et al.* 2000, Fauchald & Erikstad 2002), we found little evidence linking seabird and prey distributions at fine scales. The echosounder we used would not have detected some possible prey species, such as sand lance, which do not have a swim bladder. However, Capelin *Mallotus villosus* appeared to be the dominant forage species in the study area while sand lance, as noted, were not abundant (Haynes *et al.* 2008a).

Meso-scale habitat use

Prey relative abundance was the most important variable at the meso-scale for both murrelet density and group count, a result anticipated by the graduated analysis at finer scales—prey schools and prey relative abundance were not important at the finest scale, but became more important as bin size increased.

Stage of breeding was the second split in the regression tree for murrelet density. Murrelets were more abundant during nest initiation and incubation, even when prey relative abundance was low, than during chick rearing and postbreeding. Murrelets may be constrained to stay close to their inland nest sites during both incubation and chick rearing or they may remain in Port Snettisham to stage for inland flights after having foraged elsewhere. Lower abundance later in the season likely resulted primarily from postbreeding dispersal which, due to temporal overlap between the two stages, was grouped the with chick rearing period. Speckman *et al.* (2000) found that chick-rearing and fledging periods had the highest variability in murrelet densities at sea, with postbreeders apparently using the study area only when prey availability was high. Similarly, Becker & Beissinger (2003) found that murrelets stayed close to nesting habitat when prey availability was high and moved elsewhere when prey availability was low. Burger *et al.* (2008) reported that distance to nesting habitat was unrelated to murrelet distribution at sea, although prey availability was not considered. Low prey availability was associated with lower murrelet densities in Port Snettisham, but the interaction between prey availability and stage of breeding suggested murrelets remained close to nesting habitat despite low prey abundance early in the season.

Regression trees were based on 25 survey days—a relatively small sample size given the number of explanatory variables. Nevertheless, the model of murrelet density for T6–T9 performed well, with the regression tree based on two independent variables explaining almost 50% of the variation. At the meso-scale, unlike the finer scales considered, prey data from echosounder recordings (coupled with the variation explained by stage of breeding) were useful in explaining murrelet distribution.

Foraging activity of piscivorous seabirds has been linked to tidal cycles (Holm & Burger 2002, Zamon 2003). Although tidal stage was not selected in the tree analysis, it was related to murrelet densities in the univariate analysis, with murrelets more abundant at slack tide compared to rising and falling tides. Higher murrelet density during slack tide was also accompanied by higher prey abundance. Holm & Burger (2002) found similar results, with foraging seabirds preferring slack or moderate tidal currents. Speckman *et al.* (2000) found murrelet numbers peaked during slack tides but also during morning ebb tides. Tidal action likely affects seabird foraging by concentrating prey (Holm & Burger 2002).

As with tides, TOD was not selected in the tree models, but we found that murrelet densities were higher during afternoon–evening than during dawn–morning. This is contrary to Speckman *et al.* (2000) and Carter & Sealy (1990), who found high murrelet densities in the dawn–morning period, diminishing toward evening and dusk. As TOD was not related to prey abundance in our study, we suggest the effect on murrelet density was mediated by social or breeding behavior rather than by foraging.

Spatial scale of clustering

Univariate — At the smallest spatial scale, murrelets are known to forage mainly in pairs during breeding season (McFarlane Tranquilla *et al.* 2003), which was also the case in this study. At larger scales, Ripley's *K* analysis revealed that murrelet clustering was highly variable, with patch length ranging from 300 m to over 9 km. Mean patch lengths on different transects ranged from 1.84 to 3.96 km,

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 patch size reported for nearshore waters of Vancouver Island (Burger *et al.* 2008). The increase in patch length after breeding in Port Snettisham suggests murrelet groups foraged farther from one another when less constrained by breeding activity.

Ripley's *K* statistic assumes that samples along a transect are taken from the same statistical distribution (O'Driscoll 1998). This assumption would not be met if birds redistributed rapidly under changing environmental conditions. In a comparable study, O'Driscoll (1998) assumed that seabird distributions were reasonably stable during a transect, as was the case in this study. Because transects were essentially one-dimensional (long and narrow), patch length and clustering are somewhat misleading as measures of overall patch size. As we did not make any edge correction, longer patch lengths may be less accurate than shorter ones (O'Driscoll 1998).

Bivariate — While seabirds are known to congregate in areas where prey are concentrated (Fauchald & Erikstad 2002, Piatt *et al.* 2006), many studies have met with little success in trying to link the distributions of birds and prey (e.g. Hunt *et al.* 1992, Logerwell & Hargreaves 1996, O'Driscoll 1998, Fauchald *et al.* 2000, Skov *et al.* 2000). Others have found relationships that were spatially or temporally inconsistent (e.g. Schneider & Piatt 1986, Wright & Begg 1997, Vlietsra 2005). In this study, murrelets tracked prey at one or another scale on most days (18 of 20 surveys) and tracked prey at the finest scale analyzed (100 m) on eight of those 18 days. This suggests a relatively close temporal–spatial relationship between murrelets and prey in Port Snettisham and suggests that murrelets used the area for foraging, not only as a staging area for inland flights.

Swartzman & Hunt (2000) found that larger clusters of murres and puffins were more consistently associated with prey. In Port Snettisham, murrelets most commonly occurred in pairs. However, on days when they formed larger groups (>2.33 murrelets/group), the groups were associated with prey at a finer scale (smaller minimum scale of aggregation). The finer scale of aggregation suggests that when murrelets are in larger groups they may track prey more closely (i.e. aggregation at prey schools). Also, when murrelet group size was larger, patch length was smaller; large groups were more closely associated with prey schools and more closely spaced to other groups.

The abundance of prey affects the scale at which a predator tracks its prey (Vlietsra 2005, Fauchald 2009), and the scale of tracking affects foraging energetics (Davoren *et al.* 2002). In Port Snettisham, murrelets tracked prey over the largest range of scales (as indicated by significant aggregation proportion) when moderate levels of prey were available. This fits the nonlinear relationship proposed by Vlietsra (2005), who suggested birds employ a "sit-and-wait" approach when prey is most abundant. At intermediate prey levels, however, they approximate an ideal free distribution, resulting in high concordance between predators and prey. At lower prey levels, factors such as lack of information on prey patches (Vlietsra 2005) or activity budgets (Ronconi & Burger 2008) limit the birds' ability to track prey.

Becker & Bessinger (2003) found associations between murrelets and prey only under particular physical and biological conditions—

specifically, when prey levels were low, regional upwelling was low and sea surface temperature was high. In our study, murrelets showed a larger range of aggregation when prey was at moderate levels, suggesting they tracked prey more closely at such times. They were not tracking prey at significantly finer scales, however, as might have been expected. We infer that, regardless of prey abundance, environmental and behavioral factors, such as fluctuations in physical cues (Schneider 1982) or interspecific competition (Burger *et al.* 2008), may affect the scale at which a seabird can track its prey and thus complicate the relationship between prey abundance and tracking scale.

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