

SELECTION OF FORAGE-FISH SCHOOLS BY MURRELETS AND TUFTED PUFFINS IN PRINCE WILLIAM SOUND, ALASKA¹

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Abstract. We collected hydroacoustic and bird-observation data simultaneously along transects in three areas in Prince William Sound, Alaska, 21 July–11 August 1995. The probability of the association of fish schools with Marbled Murrelets (*Brachyramphus marmoratus*) and Tufted Puffins (*Fratercula cirrhata*) was determined through the use of resource selection functions based on logistic regression. Mean (\pm SD) group sizes were small for both species, 1.7 ± 1.1 and 1.2 ± 0.7 for Marbled Murrelets and Tufted Puffins, respectively. Oceanographically, all study areas were stratified with synchronous thermo- and pycnoclines (a water layer of increasing temperature and density, respectively, with increasing depth). Our analysis indicated that Tufted Puffins selected fish schools near their colony, whereas Marbled Murrelets selected smaller, denser fish schools in shallower habitats. We suggest that murrelets selected shallower habitats in response to lower maximum diving depths than puffins. Small feeding-groups size is discussed in terms of foraging theory and as a consequence of dispersed, low density food resources.

Key words: *Brachyramphus marmoratus*, foraging, *Fratercula cirrhata*, *Marbled Murrelets*, *Prince William Sound*, resource selection, *Tufted Puffins*.

INTRODUCTION

Determining which resources are chosen more frequently than others, relative to their abundance, is of special interest to biologists because it provides primary information about how organisms meet their requirements for survival (Manly et al. 1993). Several seabird studies have examined the selection of food resources in terrestrial habitats where resources are easily quantified (Irons et al. 1986, Pierotti and Annett 1987); however, we are unaware of forage selection studies conducted on seabirds at-sea where it is difficult to identify and quantify prey (Erwin 1977).

Hydroacoustic sampling of forage resources while simultaneously conducting bird surveys has provided much of the current information on the relationship between seabirds and their prey (Hunt 1988) and appears to be the best available

technique to determine at-sea resource selection. Several studies using these techniques have correlated seabird and forage abundances to examine the relationship between the distributions of these organisms. Potential problems remain in examining food selection because the strength of these relationships has generally weakened as the scale became finer (see Hunt et al. 1990 for review). Mehlum et al. (1996) were able to correlate Thick-billed Murre (*Uria lomvia*) abundance to forage density at a fine scale by including a prey density threshold that excluded non-preferred food items from their analysis. In examining fine scale relationships between Common Terns (*Sterna hirundo*) and forage fish, Safina and Burger (1985) did not find a relationship between predator and prey abundance but did find a significant relationship between bird abundance, depth to prey, and the presence of predatory fish. These studies suggest that marine birds may select prey based upon more factors than forage abundance or density. Furthermore,

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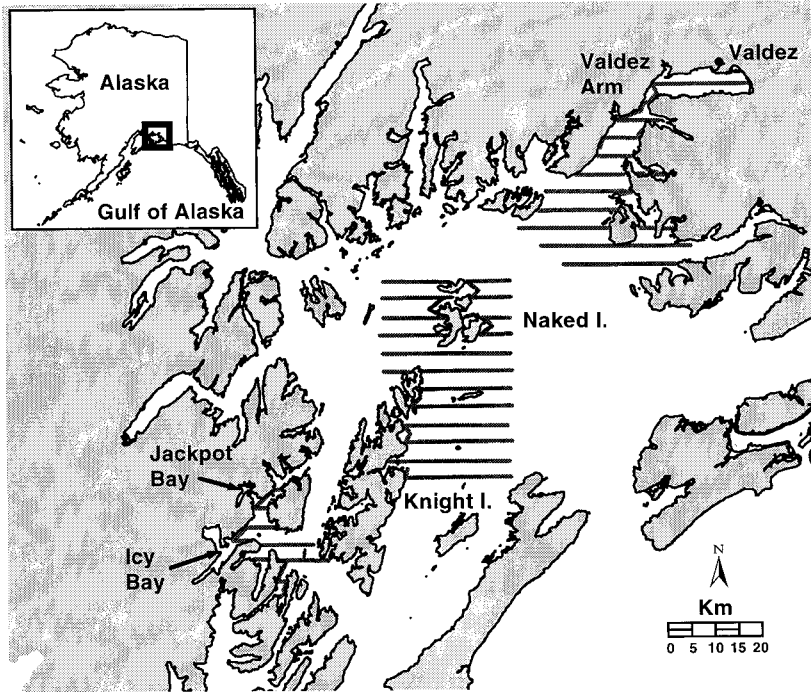


FIGURE 1. The transects (solid lines) used to conduct hydroacoustic and seabird surveys in Prince William Sound, Alaska, 21 July–11 August 1995.

studies in the tropics (Duffy 1983) and Alaska (Hoffman et al. 1981) have demonstrated that the species composition of feeding flocks was related to characteristics of associated fish schools. Therefore, we anticipated that foraging strategies of seabirds would be most apparent if we investigated seabirds' selection of fish schools by examining a suite of potential factors.

Here, we report on at-sea resource selection of Marbled Murrelets (*Brachyramphus marmoratus*) and Tufted Puffins (*Fratercula cirrhata*) in Prince William Sound, Alaska (PWS). As in previous studies, we conducted hydroacoustic sampling of forage resources while simultaneously conducting bird surveys (Hunt 1990). Our analyses differed by using fish schools as the sample unit rather than segments of transects of varying length. Thus, we were able to compare the characteristics of fish schools available to those selected.

METHODS

DATA COLLECTION

We conducted this study in PWS, an embayment of 10,000 km², located on the southern coast of

Alaska. The climate is maritime with a mean annual precipitation of 1.6 m and moderate temperatures for the subarctic. The coastline of PWS is rugged, with mountains up to 4 km in elevation and numerous fjords and tidewater glaciers. Three study sites were selected for sampling (Fig. 1): (1) the northern study area, which included Valdez Arm and Port Valdez, (2) the central study area, which included waters near Naked and Knight Islands, and (3) the southern study area, which included Icy and Jackpot Bays. In a study conducted in conjunction with ours, Haldorson et al. (1996) determined that during our study the water structure was consistently stratified, with synchronous thermo- and pycnoclines, throughout our three study areas and speculated that it was due to freshwater input from rainfall and glacier melt.

We collected hydroacoustic and bird-location data simultaneously while traveling systematically arranged transects (Anderson et al. 1979, Litvaitis et al. 1994). We used the 24-m vessel, the M/V *Pacific Star*, to replicate the hydroacoustic/bird transect survey twice between 21 July and 11 August 1995. Transect locations

TABLE 1. Transect lengths (km) for three study areas in Prince William Sound, Alaska. Zigzag transects surveyed nearshore and east-west transects surveyed open water.

Study area	Northern area	Central area	Southern area	All areas
Total east-west	99.3	152.8	23.3	275.4
$\bar{x} \pm SD$ east-west	6.6 ± 4.9	8.5 ± 4.1	2.9 ± 1.9	6.7 ± 4.6
Total zigzag	12.1	15.1	14.4	41.6
$\bar{x} \pm SD$ zigzag	1.5 ± 0.7	1.7 ± 0.8	1.8 ± 0.4	1.7 ± 0.7
East-west + zigzag	111.4	167.9	37.7	317.0

were determined by randomly selecting the starting point from 20 equally spaced points within the first 2' latitude of the southern boundary of each study area. We arranged east-west transects at 2' latitude intervals north of the initial starting latitude and added zigzag transects to increase data collection of nearshore habitats (Fig. 1). The survey consisted of 41 east-west and 25 zigzag transects. We determined the total length and mean \pm SD of both east-west and zigzag transects (Table 1).

Hydroacoustic data were collected with a 420 kHz BioSonics Model 120-121 echo-integration system with a 6° beam angle. The data were integrated for 30-sec intervals and over 1-m depth intervals, corrected for calibration, and stored on disk. Transects were run at 6 knots with the transducer towed beside the vessel. The effective range of the equipment was 65 m from the transducer. Data obtained from a commercial Global Positioning System (GPS) were written to each record. Custom software was used to scale the acoustic data using calibrated target strengths of fishes and length-weight relationships of captured fish. Volume scattering was converted to fish density using fish species and size estimates from trawl data and the following equations:

$$\text{pollock } TS = 20 (\log L) - 66 \text{ (MacLennan and Simmonds 1992)}$$

$$\text{herring } TS = 20 (\log L) - 68 \text{ (Thorne et al. 1983)}$$

$$\text{capelin } TS = 20 (\log L) - 68 \text{ (R. Thorne, pers. comm.)}$$

where TS is the calculated target strength in dB and L is the length of the fish in cm. The estimates of fish densities were converted to biomass (g m^{-3}) using the following length-weight relationships for the dominant species, where W = weight in grams and L = length in mm:

$$\text{pollock } W = (1.89 \times 10^{-6}) L^{3.272} \text{ (Haldorson$$

et al. 1996)

$$\text{herring } W = (5.007 \times 10^{-6}) L^{3.196} \text{ (L. Haldorson, pers. comm.)}$$

$$\text{capelin } W = (2.5 \times 10^{-6}) L^{3.213} \text{ (Pahlke 1985)}$$

We obtained net-sample data with a Canadian midwater herring trawl (100-m² opening) from a separate vessel directed by the hydroacoustic vessel. We selected schools for trawling which had the greatest uncertainty regarding species and/or age-class composition. These trawls were only effective on the larger schools; therefore, the samples may not have been representative of all schools. Because most targets sampled with hydroacoustics were not fished, we were unable to identify the species composition of all fish schools.

Bird observations were made from the second deck of the *M/V Pacific Star*, 8 m above the water. Continuous counts were made of all seabirds observed within 100 m of the starboard side of the vessel, the same side from which acoustic data were taken. We assigned one of the following behaviors to each bird observation: flying, on the water, on a floating object, foraging, and potentially foraging. Foraging was defined as diving for food or holding food in the bill. Potential foraging was defined as ≥ 2 associated birds on the water or circling above. Bird observations were made by scanning ahead of the ship using binoculars to avoid influence on bird activities by the vessel's presence. Data were recorded when the ship was closest to the point at which the birds were first observed. We directly recorded data into a computer file using custom software that also recorded the ship position and time for each data entry. GPS data were obtained from the same device accessed by the acoustic system. Most previous acoustic seabird studies have not included flying birds in their analysis because of the probability that birds on the wing were not associated with acoustic targets (Schneider and Piatt 1986, Piatt

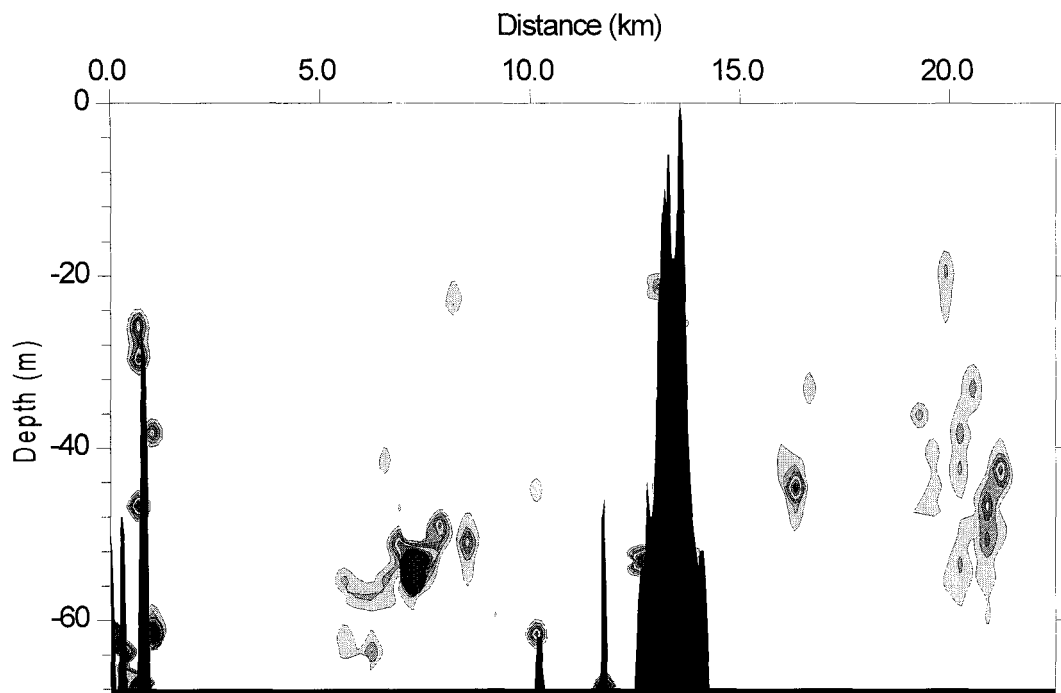


FIGURE 2. A 3D plot of hydroacoustic data collected during a survey of Prince William Sound, Alaska. Black spires represent the ocean bottom. Grey polygons represent fish schools. Darker shades of grey in polygons indicate a greater biomass density.

1990, Decker 1995). We have adapted this convention for our analysis by including only birds foraging, potentially foraging, or on the water.

DATA ANALYSIS

We displayed scaled acoustic data with contouring and three dimensional surface-mapping software (Keckler 1995). These displays represented the acoustically surveyed water as a two dimensional surface, and schools were depicted as polygons on that surface (Fig. 2). We refer to the vertical measure of polygons as school height and the horizontal measure as chord length. We multiplied the height by chord length to determine the rectangular area that would inscribe each polygon. These images also were used to determine school density, depth to top of schools, and bottom depth at school locations for values < 60 m. We ascribed categorical density values of low, medium, and high for average densities of 0.01–0.20, 0.21–0.35, and > 0.35 g m^{-3} , respectively. As a result of integrating acoustic data at 30-sec intervals, schools with a chord length of < 40 m were either not displayed or were extrapolated to 40 m. Therefore,

the minimum chord length recorded was 40 m and the smallest fish schools were not well represented. Furthermore, interpretation of school parameters was done cognizant that they represent neither mean nor maximum dimensions, rather they are values taken from the intersection of a random plane with three dimensional objects. Our data provided an index of the actual characteristics of the schools sampled by hydroacoustics.

A geographic information system (GIS) was used to examine the spatial relationships among forage-fish schools, depth, distance to shore, and locations of bird colonies. GPS data for fish schools and colony locations were converted into GIS layers. Forage-fish school data were intersected with National Oceanographic and Atmospheric Administration (NOAA) bathymetry data to determine depths for each school. Acoustic data had previously recorded depths to 60 m; therefore, GIS data for depths > 60 m were merged with acoustic bathymetric data. Digital NOAA coastline data were used to calculate distance to shore for each forage-fish school. Finally, we used GIS to calculate the distance to

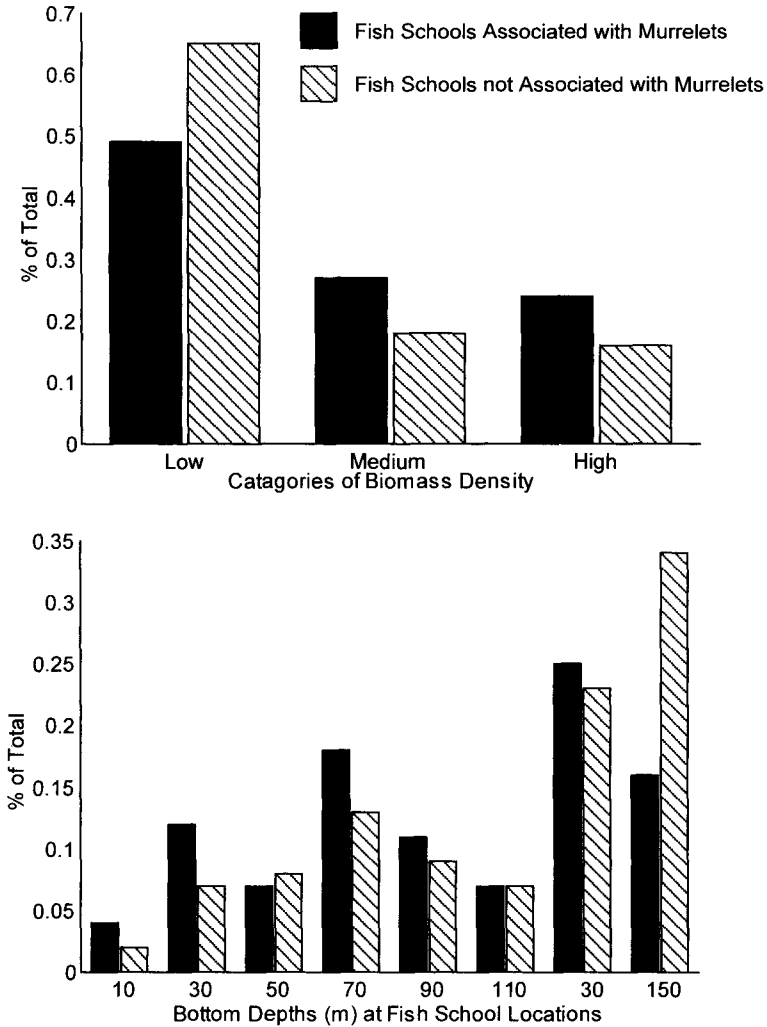


FIGURE 3. Histogram comparing depth to bottom and the categorical variable, density, for fish schools that were and were not associated with Marbled Murrelets.

the nearest Tufted Puffin colony for each school. We determined which of the forage-fish schools were associated with murrelets or puffins by searching for bird locations that were within 1/2 the respective chord length + 100 m of each school's coordinates. We selected 100 m as the distance of association to be consistent with other sources of variation: (1) the transect width allows birds up to 100-m distant to be associated with schools beneath the ship and (2) GPS data have an accuracy of about ± 100 m (Leick 1992). This measure of association does allow possible incorrect alignment of fish and birds. If misalignments were frequent, we expected them

to result in greater variability in the data and a reduction in differences between fish schools that were and were not associated with birds. Therefore, misalignments may have reduced statistical power and would only confound the interpretation of results if tests indicated there were no significant differences. Significant differences may be greater than indicated by tests.

We used resource-selection functions based upon logistic regression to model the selection of fish schools by birds (Manly et al. 1993). This analysis compared a data set of fish schools that were available to a set that were associated with birds. Conceptually, available schools include

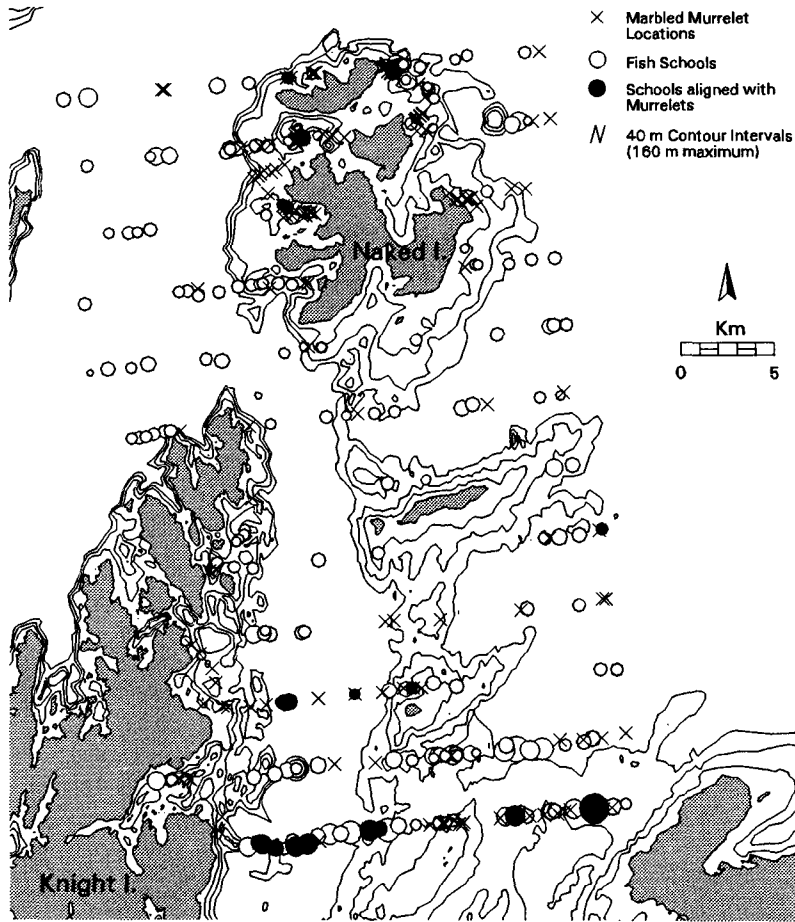


FIGURE 4. Map of the central study area depicting bathymetry and locations where Marbled Murrelets and fish schools were observed while conducting transect surveys. The diameters of circles representing fish schools are logarithmically scaled to the school's area (see Methods for definition of area in this context).

those that did not meet the selection criteria of puffins and murrelets, those that met the selection criteria but were not encountered by birds, and schools that were selected prior to or following our observations. Prior to conducting regressions, we checked variables for independence through correlation analysis. We considered $r < 0.50$ to indicate independence. We incorporated the following variables: area, depth to the top of the school, bottom depth, distance to shore, biomass density of the school, area of the school, and distance to the nearest Tufted Puffin colony. The three-level categorical variable, density, was converted to three separate binomial variables, low, medium, or high density, for these analyses. Only medium and high density levels were used in the modeling effort be-

cause knowledge of these two levels determines the value of low density. In other words, positive coefficients of either medium or high density indicated that selection was in favor of these categories when compared to low density schools. If a coefficient for either medium or high density was significant, we retained both levels in the model to fully illustrate how selection had occurred with respect to density. For the murrelet regression, distance to colony was not applicable because they are not colonial (De Santo and Nelson 1995). We considered $P < 0.05$ significant for individual independent variables within models. We began the analysis with all variables in the models and systematically deleted nonsignificant variables from the regressions singly and ordinally, beginning with highest P values,

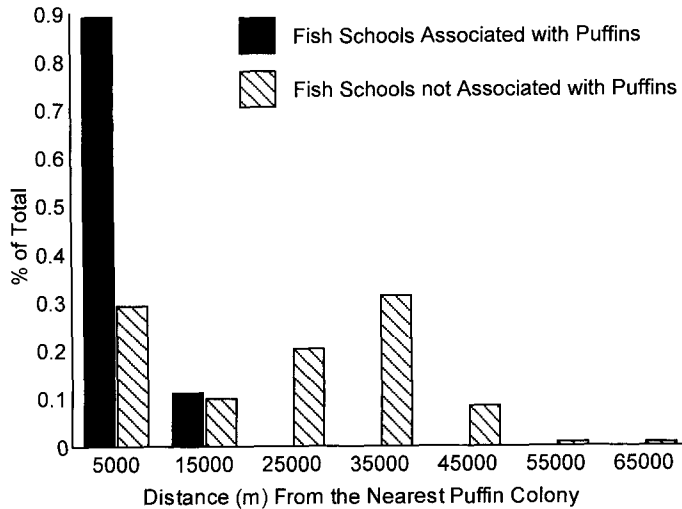


FIGURE 5. Histogram comparing the distance to the nearest colony for fish schools that were and were not associated with Tufted Puffins.

until all remaining terms in the model were significant. The models selected by this method were checked to determine if they had the lowest Akaike's information criterion (AIC) value (Akaike 1973) of all possible configurations. The AIC statistic describes fit of the model while penalizing for including variables that explain minimal error. We considered models to be significant if, based on the likelihood ratio test, the covariates explained 95% of the variation ($P \leq 0.05$).

We anticipated that a confounding source of bias may have resulted from a greater probability of birds aligning with fish schools that had a greater chord length, if bird distributions were random. To determine if this bias had occurred, we plotted both the number of fish schools associated with birds by chord size groups and the number we expected if alignment were proportional to length. Groups of expected to observed also were compared with a chi-squared test (Zar 1984). When this analysis indicated significant differences, we suspected that variables that were correlated with chord length might indicate spurious results. To further investigate this bias, we conducted a randomization test (Manly 1991) of the regression coefficient under the null hypothesis that schools are selected proportional to size. We used our actual data to conduct the trials. Seventy schools were selected at random with probability of selection proportional to size. These schools were assigned as the used set and

the remaining schools were assigned to the available set. Logistic regression was then run and the resulting regression coefficients were saved from each sample. We conducted 1,000 iterations of the randomization trial. If 95%, i.e., 950, of the coefficients were greater than our original coefficient, we considered the differences to be significant and modified the original model to correct for bias. We assumed that the mean value of the coefficients obtained from our randomization trials to represent idealized conditions in which birds selected prey in proportion to their availability. We then determined how observed selection differed from the idealized by subtracting the mean coefficient obtained from the randomization trials from the original value. The resulting difference then replaced the original coefficient in the model. Means are reported \pm SD.

RESULTS

We observed 554 Marbled Murrelets and 146 Tufted Puffins during our surveys. The group sizes were small for each species, 1.7 ± 1.1 and 1.2 ± 0.7 for Marbled Murrelets and Tufted Puffins, respectively. The total sighting locations were 326 for murrelets and 122 for puffins.

Of the hydroacoustically sampled forage-fish schools ($n = 615$), 79 had birds associated with them. Marbled Murrelets aligned with 70 schools and Tufted Puffins with 9. Mean values for fish school parameters were 14.5 ± 17.6 m

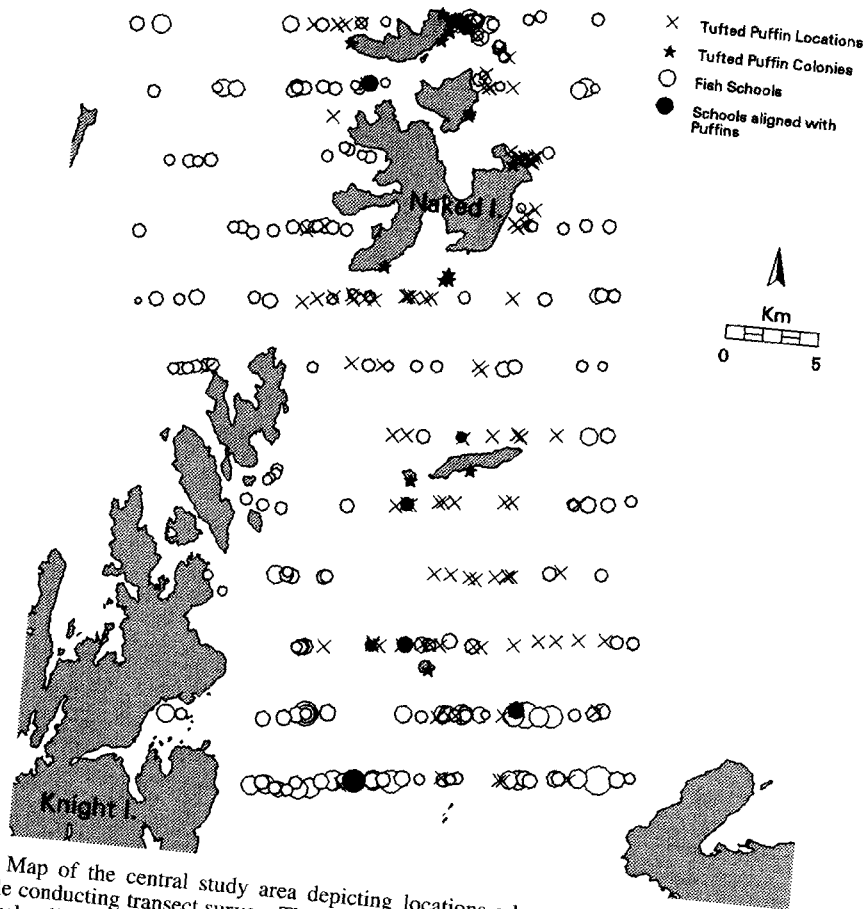


FIGURE 6. Map of the central study area depicting locations where Tufted Puffins and fish schools were observed while conducting transect survey. The diameters of circles representing fish schools were scaled to the school's area (see Methods for definition of area in this context).

for depth to the top of the school, 109 ± 43 m for total depth at the school, $2,299 \pm 2,051$ m for distance to shore, and $1,842 \pm 4,936$ m² for area. Net sampling indicated that the principle forage species were juvenile walleye pollock (*Theragra chalcogramma*), capelin (*Mallotus villosus*), sand lance (*Ammodytes hexapterus*), and juvenile pacific herring (*Clupea harengus*). Correlation analysis indicated that all of the variables included in our modeling were independent ($r < 0.5$). The resource-selection models indicated that murrelets selected schools in shallower water, that were greater in density (Figs. 3 and 4) and area. Tufted puffins selected schools that were near their colonies (Figs. 5 and 6). Both models were significant and had AIC and concordance values of 423.8 and 66.3%, respectively, for the Marbled Murrelets and 75.2 and 89.9%, respec-

tively, for the Tufted Puffin models. Our comparison of expected number of birds associated with fish to observed, by chord length, indicated significant difference in the distributions ($\chi^2_3 = 42.8$, $P < 0.001$) (Fig. 7). We then determined that area, within the murrelet model, was correlated with chord length ($r = 0.90$) and proceeded with a randomization evaluation of this source of bias (Manly 1991). All 1,000 iterations of our randomization tests produced coefficients of area larger than the corresponding coefficient in our original model, indicating $P < 0.001$. We adjusted the area coefficient in the model by subtracting our mean randomization value, 0.00037 ± 0.00008 , from the original. The modification reversed the sign of the coefficient, indicating that selection was for smaller fish schools when compared to those available (Table 2).

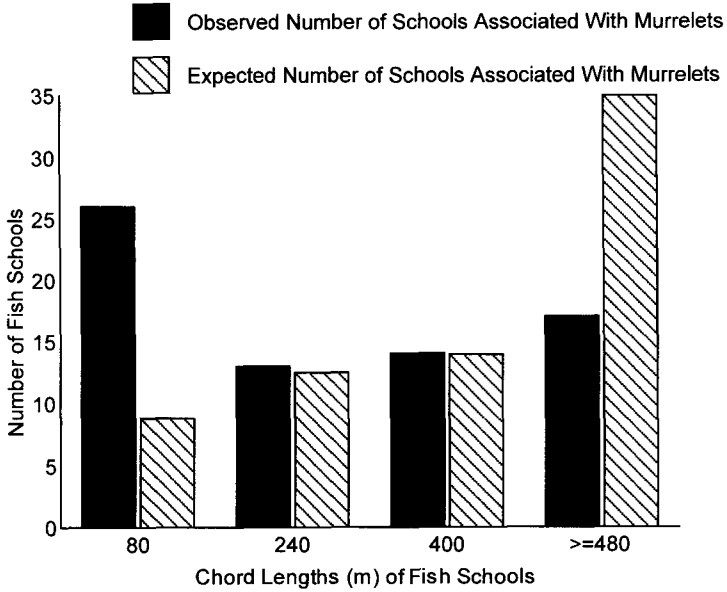


FIGURE 7. Histogram comparing the expected number of birds associated with fish schools to the observed numbers for chord-length size classes.

DISCUSSION

By examining the characteristics of fish schools we were able to develop resource selection models for Tufted Puffins and Marbled Murrelets. The two models that we obtained contained different variables, suggesting that these species use different strategies to obtain forage. The models indicated that puffins foraged near their colonies and murrelets preferred shallow water habitats and within those habitats selected smaller and denser schools. These models support our hypothesis that prey selection is based upon multiple factors and is best studied through a multivariate approach.

Several studies have demonstrated that dense seabird concentrations and foraging is frequently associated with advection or turbulence-caused prey concentration (Hunt 1990). Conversely, we suggest that the absence of advection and the presence of stratification, as in PWS, results in comparatively lower density or dispersed forage and in turn, lower seabird numbers and smaller feeding group sizes. Direct support of this intuitive hypothesis is sparse; however, in describing a system with low seabird density, Robertson (1977) suggested that a stratified water structure within the Strait of Georgia, due to freshwater input, and low density of preferred forage fish

was linked to low avian numbers. Forage fish (Piatt et al., in press) and seabird densities (Kendall and Agler 1996, U.S. Fish and Wildlife Service, Anchorage, Alaska, unpubl. data) within PWS are low when compared to the advected systems of Cook Inlet and the Pribilof Islands, Alaska. We suggest that the dominant seabird species of PWS should have resource selection functions that allow efficient utilization of dispersed, low density forage associated with oceanographic conditions.

PWS is one of Alaska's principle nesting areas for Marbled Murrelets (Piatt and Ford 1993) and they are the area's most abundant seabird species (Agler et al. 1994). This may indicate that although Marbled Murrelets are likely to benefit from the concentration of prey and localized increase in productivity that result from advection (Hunt 1995), it is not necessary for maintaining a local population. There are no other studies that have related oceanographic structure to murrelet foraging (Hunt 1995); however, Piatt and Ford (1993) have suggested that tidally mixed open waters provide poor foraging habitat when compared to stratified nearshore water. Our observations of association with shallow water and small group size are consistent with the findings of studies conducted elsewhere

TABLE 2. Models of the likelihood that fish schools ($n = 615$) will be associated with diving birds using school characteristics as independent variables. The murrelet model has been adjusted for bias due to the greater probability of birds being associated with larger schools.

No. schools not associated with birds	No. schools associated with birds	Model	Model P
545	70	Murrelets ^a = $-0.01T\text{Depth}^b(0.0004)^c - 0.00037\text{Area}^d(0.03) + 0.62M\text{Density}^e(0.05) + 0.53H\text{Density}^f(0.12)$	<0.001
606	9	TPuffins ^g = $-0.00026D\text{Colony}^h(0.02)$	<0.001

^a The probability of selection by Marbled Murrelets.

^b Total water depth.

^c P value of the associated independent variable.

^d The chord length * the mean height of the school.

^e Selection for medium-density fish schools over low-density schools. If either medium- or high-density variables were significant, then both were retained in the model.

^f Selection for high-density fish schools over low-density schools.

^g The probability of selection by Tufted Puffins.

^h Distance to the nearest Tufted Puffin colony.

(Carter and Sealy 1990, Strachan et al. 1995) and within PWS (Kuletz et al. 1994). We suggest that the Marbled Murrelet's ability to forage on small schools of broadly distributed prey that can be associated with stratified water, and abundant nesting habitat (Piatt and Ford 1993), may account for its dominance of the PWS seabird population.

In a study conducted sympatric and synchronous to ours, Piatt et al. (in press) examined the food habits of Tufted Puffins and found that they had a diverse diet and did not take forage items in proportion to their availability. Our resource selection model for Tufted Puffins contained only a location variable (distance from the nearest Tufted Puffin colony) and did not detect the selectivity indicated by Piatt et al. Tufted Puffins' diverse diet suggests that selectivity by school characteristics may be complex, and our sample size was inadequate to resolve these intricacies. The combined results of Piatt et al's. and our study suggest that Tufted Puffins select fish schools of varying characteristics and flight distances from their colony is a major component of foraging decisions.

Elsewhere, Tufted Puffins have been observed to forage preferentially in stratified water (Haney 1991), in close proximity to their colony (Cody 1973, Vermeer et al. 1987), and in small foraging groups (J. F. Piatt, unpubl. data), suggesting that our observations are typical for the species. Although Tufted Puffins foraged near their colony they did not demonstrate a preference for shallow water. This difference in habitat selection by murrelets and puffins may be the result of differences in their maximum diving depths. Although the specific diving depths of

these species are unknown, an allometric relationship between body size and maximum diving depth (Piatt and Nettleship 1985, Burger 1991) suggests that the larger Tufted Puffin (DeSanto and Nelson 1995) should be capable of deeper dives. Hence the larger species is less constrained by water depth.

Our results suggest that Tufted Puffins and Marbled Murrelets used different foraging strategies to locate forage-fish schools. However, both species foraged extensively as individuals or in small groups. Similarly, Irons (1992) observed that Black-legged Kittiwakes (*Rissa tridactyla*) in PWS also foraged as individuals or in small dispersed groups. We suggest that these common foraging behaviors are a response to the low density and dispersed prey of PWS. This strategy contrasts sharply with previous studies in which most foraging occurred in larger feeding flocks (Hoffman et al. 1981, Duffy 1983). These differences may be consistent with a hypothesized allometric relationship between school size and feeding group size (Duffy 1983) if the fish schools associated with flocks in previous studies were larger than those in PWS. Small group sizes observed in PWS can be best explained in the context of foraging theory (Stephens and Krebs 1986). For this discussion we consider fish schools to be forage patches. We also assume that individual birds make decisions on whether to enter patches encountered while foraging to maximize their net energy gain. We suggest that the profitability of an individual joining a feeding flock is greater when forage is more abundant and/or aggregated by oceanographic structure than when food is broadly distributed in smaller patches. Small patches may

quickly be overexploited by feeding flocks with minimal net energy return to individual foragers. In addition, Maniscalco and Ostrand (in press) examined behavior at relatively rare mixed-species feeding flocks in PWS and determined that kleptoparasitism among Black-legged Kittiwakes (*Rissa tridactyla*) was higher than reported elsewhere in the literature (see Furness 1987 for review). A high rate of kleptoparasitism suggests greater energy costs due to competition and social interaction at feeding flocks. Social costs could exacerbate the effects of low energy availability at small patches. A greater return for energy expended foraging might be gained by foraging as individuals or small groups and avoiding competitive feeding flocks at small patches.

In conclusion, by employing new analysis techniques to established data collection methods, we have gained initial insight into at-sea resource selection by birds. We believe these techniques will be of value in examining the complex relationship between seabirds and their prey when applied to other species and at other locations.

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