FISH SCHOOL SELECTION BY MARBLED MURRELETS IN PRINCE WILLIAM SOUND, ALASKA: RESPONSES TO CHANGES IN AVAILABILITY

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SUMMARY

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We sought to determine how fish school selection by Marbled Murrelets *Brachyramphus marmoratus* changed as the availability of forage fish fluctuated among years within Prince William Sound, Alaska. Hydroacoustic and bird-location data were collected simultaneously while traveling systematically arranged transects during the summers of 1997, 1998 and 1999. We determined the number, location, species composition and general characteristics of all fish schools within the hydroacoustic data set. We determined which schools were associated with murrelets and compared their characteristics to the non-associated schools through multivariate logistic regression modeling. During 1997 when lipid-rich Pacific Herring *Clupea pallasi* were abundant, murrelets selected smaller schools near the surface. In 1998 the schools detected by hydroacoustics were bigger schools of large herring, located in deeper water, and further from the surface than those observed in 1997 and 1999, and murrelets were not associated with those schools. Gadids (predominantly Walleye Pollock *Theragra chalcogramma,* but also Pacific Cod *Gadus macrocephalus* and Saffron Cod *Microgadus proximus*, all low-lipid species, were the most abundant school type in 1999, and herring were less numerous than in the previous years. Murrelets responded to the 1999 changes in availability by selecting for herring, while school size and depth to schools were less important in choosing food resources. We suggest that murrelets responded to changes in the availability of food by making choices that maximize their net energy intake, as predicted by foraging theory. We further observe that resource selection studies that utilize data from one point in time may not demonstrate the full range of possible models.

Key words: Marbled Murrelet, *Brachyramphus marmoratus,* distribution, food, foraging, Alaska

INTRODUCTION

Foraging theory for central place foragers (Stephens and Krebs 1986) suggests that the energy return expected from a food item is weighed against the cost of obtaining that item when choosing which food source to pursue. Within Prince William Sound (PWS), Alaska, seabirds consume several different food items (Kuletz *et al.* 1997) which vary in energy content (Anthony & Roby 1997, Anthony *et al.* 2000). Of the available forage fishes, Pacific Herring *Clupea pallasi* rank among the richest in lipid content and Walleye Pollock *Theragra chalcogramma* near the lowest (Anthony & Roby 1997, Anthony *et al.* 2000). In feeding experiments, Black-legged Kittiwake *Rissa tridactyla* chicks fed on Walleye Pollock developed more slowly than those fed equal amounts of herring (Romano 2000). Studies conducted on free-ranging seabirds in PWS also demonstrate the importance of high-lipid fishes. Golet *et al.* (2000) found that Pigeon Guillemots *Cepphus columba* had higher reproductive success and their chicks grew faster when they provisioned their young with a higher percentage of high-lipid fishes. Therefore, we expect seabirds to select herring over pollock when the cost of obtaining both food items is comparable. Measures of resource selectivity (Manly *et al.* 1993) should show a preference for herring. We also speculate, based on foraging theory (Stephens & Krebs 1986), that when herring schools are plentiful, seabirds will choose herring schools that are the easiest to obtain. Conversely, when herring become rare or the cost of obtaining

herring exceeds the energy return that can be expected, and food sources which are more profitable to obtain are available, seabirds will switch to other prey items.

Previously Ostrand *et al.* (1998) and Maniscalco *et al.* (1998) developed foraging resource selection models for seabirds; however, their work was limited to one year of data and they were not able to identify the composition of schools to species. Therefore, they were unable to assess how resource selection might change as the species composition and availability of food resources changed. Advances in hydroacoustic hardware technology, data processing, and the availability of classification statistical methods have facilitated limited identification of fish schools (MacLennan & Holliday 1996), allowing us to add forage species to the suite of variables considered by the previous studies. By collecting data over three years we were able to examine how selection of fish schools by seabirds changed among years. We were also able to quantify differences in food availability and speculate on how food selection has responded to changes. We used Marbled Murrelets *Brachyramphus marmoratus* as the focal species because they are the most abundant species in PWS (Agler *et al.* 1994). Their propensity to sit on the water at foraging sites (Ostrand 1999) allowed us to determine if they were associated with fish schools detected through hydroacoustics (Ostrand *et al.* 1998).

MATERIALS AND METHODS

Study area
We conducted this study in PWS, an embayment of *c.* 10 000 km², located on the Gulf of Alaska. The climate is maritime with a mean annual precipitation of 1.6 m and moderate temperatures for the sub-arctic. The coastline is rugged, with mountains up to 4000 m elevation, numerous islands, fjords, and tidewater glaciers. Nearshore bathymetry is characterized by both shallow water shelves and steeply sloping bottoms. Four study areas were selected which included most of the marine habitats found in PWS: (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, (3) the southern study area, which included Icy and Jackpot bays, and (4) the north shore of Montague Island (Fig. 1).

Data collection

Study designs
As in previous seabird food selection studies (Ostrand *et al.* 1998, Maniscalco *et al.* 1998), we collected hydroacoustic and bird-location data simultaneously on transects (Anderson *et al.* 1979, Litvaitis *et al.* 1994). Previous studies conducted within PWS, which compared use versus availability, indicated that murrelets preferred shallow water (Ostrand 1998) and that forage fish were most abundant near shore (Haldorson *et al.* 1996); therefore, we chose to conduct a nearshore survey. The survey utilized 1-km by 12-km shoreline blocks located within the four study areas (Fig. 1).
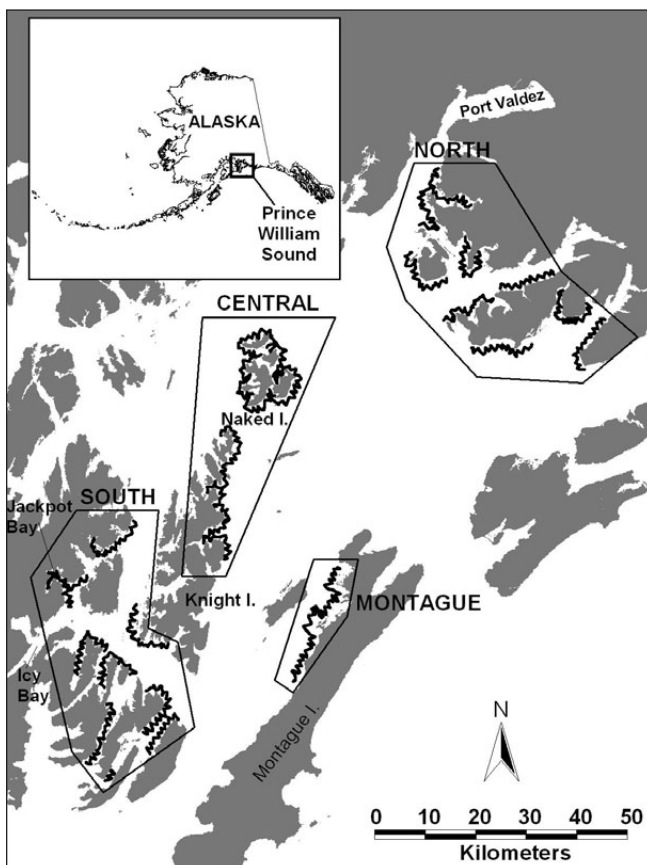

Fig. 1. The survey route for hydroacoustic and seabird data collection in Prince William Sound, Alaska, 1997–1999.

Contiguous blocks were delineated, which included all available shoreline within the study areas. Due to the large extent of the northern and southern areas and the impracticality of sampling their entire shoreline, alternate blocks and one and two additional randomly selected blocks were deleted from the North and South areas, respectively. All possible blocks were retained in the Central and Montague areas. The final study design contained 9, 8, 8 and 2 blocks in the North, Central, South, and Montague Island areas, respectively. Within each block, 20 continuous *c.* 1.2-km transects were laid out in a zig-zag pattern (Fig. 1). The surveys were conducted during 15–27 July 1997, 13–31 July 1998, and 9–18 July 1999. The length of the murrelet/hydroacoustic survey in 1997 and 1999 was 684 km, with 224 km, 186 km, 213 km, and 60 km in the North, Central, South, and Montague study areas, respectively. The 1998 survey was shortened in the South and Montague Island areas by a total of 3.5 study blocks or 120 km. (see Haldorson *et al.* 1999 for details on where deletions were made).

Fish school data collection
These surveys utilized 18-m commercial purse seiners during 1997 and one week in 1998 and a 22-m research vessel during the remainder of 1998 and 1999 for hydroacoustic and bird-location data collection. Hydroacoustic data were collected with a single-beam 120 kHz BioSonics DT4000 system with a six-degree beam angle at a rate of three pings per second. Transects were run at six knots with the transducer towed along the starboard side of the vessel 1 m below the surface. Data were collected to a depth of 117 m from the transducer. To ensure that hydroacoustic data were comparable among years, field calibrations were conducted on the transducer with a standardized target each year, prior to and during each survey. Location data were obtained from a precision lightweight global positioning receiver (PLGR). PLGR units have a 95% probability of a horizontal position accuracy of <4 m (Karsky *et al.* 2000).

The species composition of selected fish schools, which had been sampled hydroacoustically, was determined by netting or through the use of underwater video (Thedinga *et al.* 2000). Both forms of data collection utilized a second 18-m commercial purse seiner as a catch vessel. A 200-m long by 20-m deep purse seine with a 25-mm stretch mesh was the primary catch gear, but some samples were collected with dip and cast nets. Schools selected for identification were those that had the greatest level of uncertainty associated with species composition based on observed signal on sounder display. We selected a demarcation between large and small herring at a length of 130 mm to be consistent with Burkett (1995), who surmised that herring longer than 130 mm were not consumed by murrelets.

Bird data collection
Bird observations were made from the wheel-house located on the second deck, about 3 m above the water. Continuous counts were made of all seabirds observed on the water utilizing 100-m strip transects, 50 m either side of the vessel (Schneider & Piatt 1986, Kendall & Agler 1998). Bird detections were made by a single observer scanning up to 100 m ahead and above the ship with binoculars. Data were recorded when the ship was closest to the point at which the birds were first observed so as to provide the most accurate association between bird observations and hydroacoustic data. A second observer was added when bird concentrations were encountered and data recording became challenging. We recorded data directly into a computer file using

custom software that also recorded the ship position with each data entry. GPS data were obtained from the same PLGR accessed by the acoustic system.

Data analysis

Correction for 1998 reduced survey length
Because of the reduction in survey extent, data sums from 1998 are given as absolute numbers and as values corrected to the 1997 and 1999 efforts, which were determined by the formula

Corrected value =
('97 & '99 survey length / '98 survey length) x observed '98 sum
or,
Corrected value = 1.15 x observed '98 sum

Classification and characterization of fish schools
Hydroacoustic data were processed using Echoview (SonarData, Tasmania, Australia) software (version 1.51.20) utilizing the school detection feature. This feature searched the hydroacoustic data for schools which we defined as fish aggregations detected for >4 m to be consistent with the PLGR accuracy. We selected settings within Echoview to output all available variables that described both the backscatter and dimensional attributes of each school. Schools that had been sampled in the field were classified to species while those that had not been sampled received a default classification of "unidentified." Species classifications of identified schools were then reduced to the all inclusive groupings: herring, gadids and "other." These groupings became training data sets within S-plus (MathSoft 1999) to develop classification tree models (Chambers & Hastie 1992, Bell 1996) for each year. Tree models provide an alternative to linear and additive logistic models for classification problems. Tree models are fit by successively splitting the data to form homogeneous subsets. The result is a hierarchical set of decision rules which can assign classification in a manner similar to the application of dichotomous keys. A jackknife procedure, which compared field identification to model predictions of the training data set, was used to estimate correct-classification rates: (number correctly identified / total schools) × 100 (Ostrand & Howlin 2000). We used a minimum acceptable correct-

TABLE 1
Number of fish schools detected by hydroacoustics and identified to species via fishing or underwater video camera inspection during hydroacoustic surveys of Prince William Sound, Alaska

Species/size	1997	1998	1999
Large Herring[1]	6	9	
Small Herring[1]	7	1	13
Adult Rockfish (*Sebastes* spp.)	3		
Salmon		1	
Sandlance	3		1
Gadids[2]			36

[1]The demarcation between large and small Herring was a length of 130 mm.
[2]Gadids are predominantly *Theragra chalcogramma,* but also juvenile *Gadus macrocephalus* and *Microgadus proximus.* Approximate length was 51.5±1.7 mm for juvenile schools, with one additional school of adults whose approximate length was 378.8±41.0 mm.

classification rate of 75% to guide tree selection. The models were used to ascribe a species classification to all hydroacoustically sampled schools (Ostrand & Howlin 2000).

Fish school selection by murrelets
We determined which of the forage-fish schools were associated with murrelets by searching for bird locations within 50 m of the edge of each fish school. We selected 50 m as the distance of association to be consistent with the transect width which allowed birds up to 50 m distant to be associated with schools beneath the ship.

To describe fish school selection by year we conducted multivariate logistic regression, which compared the characteristics of fish schools associated with murrelets (used resources) to all other schools detected by hydroacoustics (unused resources) by year (Manly *et al.* 1993). In this case, unused resources included schools that did not meet the selection criteria of murrelets, those that met the selection criteria but were not encountered by birds, and schools that were selected by birds prior to or following our observations. Rather than conduct our modeling with all possible variables, we limited analysis to include only those variables that our knowledge of murrelet biology indicated might be important, as suggested by Burnham and Anderson (1998). Murrelet dive depth may limit access to forage (Burger 1991), and they forage selectively in shallow habitats (Carter & Sealy 1990, Ostrand *et al.* 1998); therefore, we included total depth of water, depth to each fish school, and depth below each school as variables. Ostrand *et al.* (1998) demonstrated that murrelets selected small schools; therefore, we have included school area as calculated by the Echoview software. The school area algorithm assumed that schools were symmetrical to the two-dimensional profile recorded in the hydroacoustic data. Day & Nigro (2000) determined that distance from shore was a factor in foraging habitat selection by murrelets, and that factor was included. Ostrand *et al.* (1998) also determined that school density was a factor in selection. However, converting backscatter to density requires knowledge of the mean length of fish within schools (MacLennan & Simmonds 1992), which we were unable to determine for all schools. Therefore, we have included mean backscatter for each school as a surrogate for density. Finally, because energy content of fish varies among taxa (Anthony & Roby 1997, Anthony *et al.* 2000) we have included species of the school. Species were entered into the models as binary variables: herring or not herring (all years) and gadids or not gadids (1999 only). Gadids were observed only in 1999. We developed model sets composed of all possible combinations of variables excluding interactions and higher order terms (127 models for 1997 and 255 for 1999). Models were not developed for 1998 due to the small number of schools that were observed associated with murrelets. We fitted logistic regression to all equations within the model set. These were ranked based upon Akaike's information criterion corrected for small sample sizes (AICc (Akaike 1973, Burnham & Anderson 1998)). For each year we determined importance values for each independent variable using the model sets (Burnham & Anderson 1998).

To compare the variables that describe fish schools, fish school abundance, murrelet abundance (total observed), sightings of murrelets (observations of individuals or groups) and murrelet group size, we used the study block as a sample unit. Total values per block were compared among years with single-factor ANOVAs and Tukey multiple comparison tests (SAS 1996). We considered $P < 0.05$ significant. Means are reported ±standard error (s.e.).

RESULTS

Species composition and size of the field-identified schools detected by hydroacoustics differed among years (Table 1). The number of schools that were field-identified within a year reflected sampling effort, rather than abundance of fish schools. During 1997 there was a mix of schools composed of large or small herring; in 1998 all but one identified school was composed of large herring; and in 1999 all herring identified were small. In all years and in all catches, the composition of schools was dominated by a single species and a single age class. Juvenile gadids were identified among the hydroacoustically sampled schools only in 1999. The gadids were predominantly juvenile Walleye Pollock, but also juvenile Pacific Cod *Gadus macrocephalus* and Saffron Cod *Microgadus proximus.* The mean fish length was 51.5±1.7 mm for juvenile schools; one additional school of adults had a mean fish length of 378.8±41.0 mm (Thedinga *et al.* 2000). The Other group consisted of schools of juvenile salmon *Oncorhynchus* spp. and adult rockfish *Sebastes* spp.

For the tree classification analysis, the estimated correct-classification rates of schools to species were 76%, 79% and 78% for 1997, 1998 and 1999, respectively. The trees had 2, 2 and 6 terminal nodes for 1997, 1998 and 1999, respectively. Tree classification analysis did not assign a size classification to schools in the hydroacoustic data sets. The sizes of fish within schools were known only for those sampled with net or video gear.

More fish schools were detected by hydroacoustics in 1999 than in previous years; however significant differences were observed only between 1999 and 1998 (Table 2). Due to the numerical dominance of gadids, the fewest schools were identified as herring by the tree classification for 1999. In 1998 the detected schools were significantly larger and were observed at greater depth in deeper water (Table 3).

Significantly more sightings per block, birds per block, and larger group sizes of murrelets were observed in 1997 than in the following years (Table 4), but these variables did not differ significantly between 1998 and 1999. There were 12, 3 and 13 schools 50 m from a murrelet sighting for 1997, 1998 and 1999, respectively. These schools associated with murrelets ("used") were compared to other "unused" schools in the development of selection models. Due to the small number of used schools in 1998, no models are presented for that year. The reduction in the extent of the survey length, the number of fish schools (Table 2) and murrelet observations (Table 4) may also have contributed to the small number of alignments; however the survey total length had been reduced by 18%, while the number of schools associated with murrelets was 71% fewer.

The best fish school selection models, based on AICc evaluation, as well as the order of variables ranked by importance values, differed between 1997 and 1999 (Table 5). Herring ranked five (low) and

TABLE 2
Number of fish schools sampled by hydroacoustics during three years in Prince William Sound, Alaska

Year	Fish schools	Herring schools	Fish schools/ block	Herring schools/block
1997	149	98	5.5±0.8 ab[1]	3.6±0.6 a[1]
1998	107 (123)[2]	54 (62)[2]	4.3±1.2 b	2.3±0.7 ab
1999	180	25	8.4±1.3 a	0.9±0.4 b

[1]Values sharing a common letter were not significantly different (*P* > 0.05).
[2]Standardized values account for shorter survey conducted in 1998 (see Materials and Methods).

TABLE 3
Characteristics of all fish schools detected by hydroacoustics during three years in Prince William Sound, Alaska. See Table 2 for sample sizes

Year	Distance to shore (m)	Approx. backscatter (dB)	Depth to school (m)	Depth school (m)	Total depth (m)	Area below (m²)
1997	655.3±37.4 ab[1]	−62.68±0.32 b[1]	36.5±1.8 b[1]	15.2±1.7 a[1]	51.8±1.9 b[1]	36.4±6.0 b[1]
1998	587.6±36.1 b	−62.84±0.31 b	43.8±2.1 a	19.9±2.3 a	63.7±2.1 a	77.1±17.8 a
1999	717.4±28.8 a	−61.22±0.36 a	30.4±2.1 c	13.8±1.7 a	44.2±2.4 c	36.2±6.8 b

[1]Values sharing a common letter were not significantly different among years (*P* > 0.05).

TABLE 4
Numbers of Marbled Murrelets observed on surveys during three years in Prince William Sound, Alaska. Blocks were 1-km × 12-km sampling units composed of 20 1-km transects

Year	Sightings	Total birds	Sightings/block	Birds/block	Bird group size
1997	603	2108	22.3±3.9 a[1]	78.1±15.2 a[1]	3.5±0.3 a[1]
1998	189 (217 std.)[2]	527 (606 std.)[2]	8.2±1.3 b	22.9±6.6 b	2.8±0.4 b
1999	331	767	12.3±1.2 b	28.4±4.6 b	2.3±0.1 b

[1]Values sharing a common letter were not significantly different (*P* > 0.05).
[2]Standardized (std.) values account for a shorter survey in 1998 (see Materials and Methods).

one (best), among all independent variables for 1997 and 1999, respectively. The best model for 1997 indicated an inverse relationship between selection of schools by birds, and school area and depth to school. The best model in 1999 contained only herring as an independent variable. A graphic comparison of the variables within the best models is presented in Fig. 2.

DISCUSSION

The modeling efforts for the 1997 and 1999 data indicated that fish school selection by birds differed between years (Table 5 and Fig. 2). Our findings for 1997 suggest that murrelets were responding to herring abundance by selecting preferable-sized schools (smaller) and ease of access (shallow depth to school), and, consistent with our predictions based on foraging theory, they took mostly herring (Fig. 2). In 1999 there was a significant decline in the availability of herring and most of the available fish schools were composed of gadids. Murrelets appeared to respond to the shift in forage availability by altering their selection preferences.

Selection for herring became dominant and depth to school and school area ranked seventh and eighth in importance, respectively. We suggest that when the more energy-rich herring were less available and energy-poor gadids were abundant, murrelets responded by choosing the higher energy content food source and being less selective with regard to depth to school and school size, again consistent with our predictions based upon theory for central-place foragers (Stephens & Krebs 1986).

We were unable to model fish school selection with the 1998 data due to the small number of birds associated with fish schools. Our comparison of reduction in survey length in 1998 to the reduction in bird/fish association suggested that altered sampling did not explain the small number of murrelet foraging observations. The lack of association suggests that murrelets were not selecting the fish schools that were sampled by hydroacoustics during the 1998 survey. Differences in the data describing schools sampled by hydroacoustics in 1998, compared to the other years, indicates plausible explanations as to why murrelets did not select from the
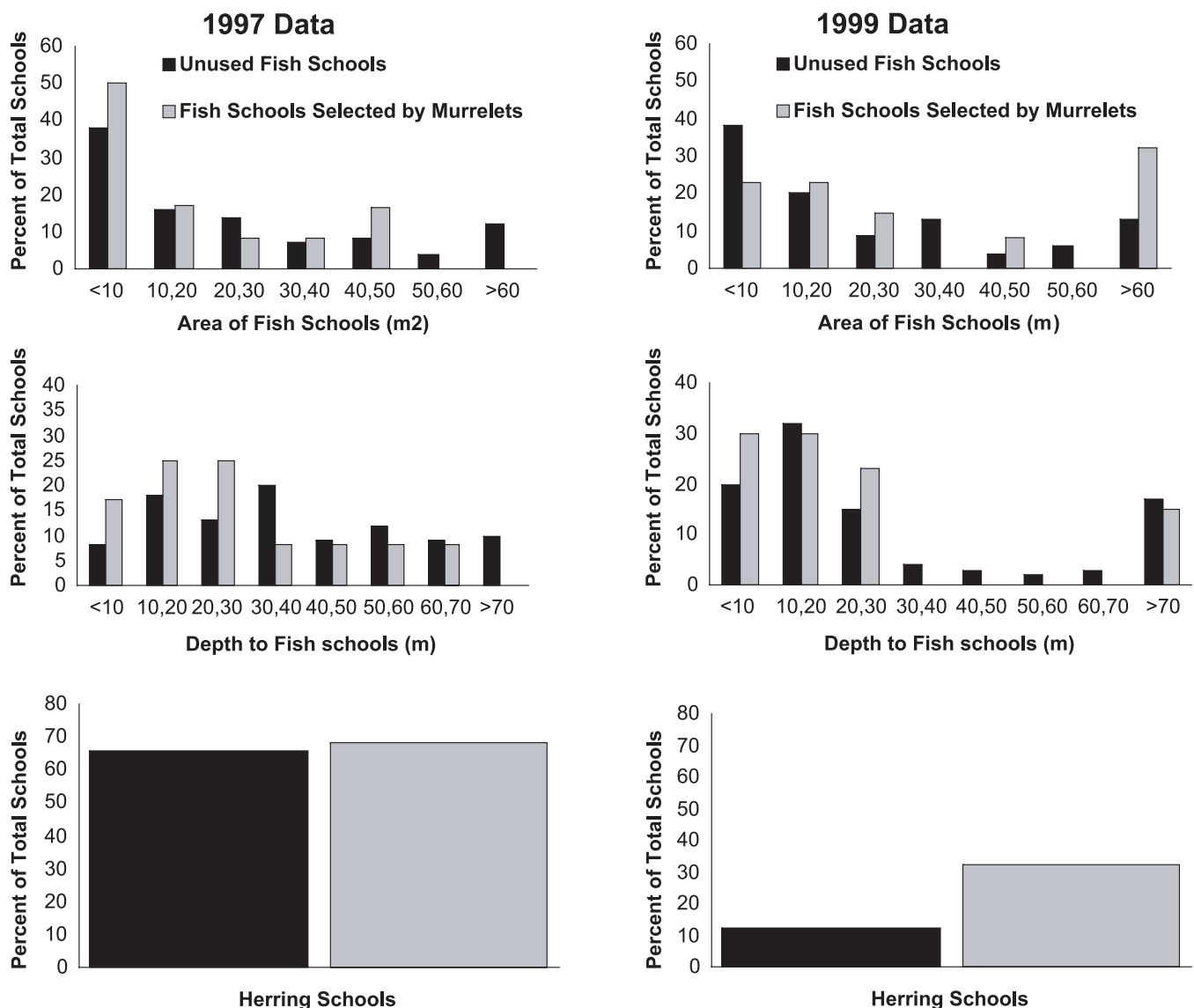

Fig. 2. Comparisons of characteristics of used and available fish schools for the summers of 1997 and 1999. Area of schools and depth to schools were the variables in the best logistic model for 1997, and herring was the only variable in the best 1999 model.

available fish schools. In 1998 schools were significantly larger, further from the surface, and in water of greater depth than the other years (Table 3). The field identification data (Table 1) suggest that most herring schools were composed of large fish. The 1997 model (Table 5, Fig. 2) and Ostrand *et al.* (1998) indicated that murrelets selected for smaller schools than the available mean. Feeding in small groups (Table 4, also Carter & Sealy 1990, Ostrand *et al.* 1998, and Day & Nigro 2000) may be a response to small schools of dispersed prey typical of PWS (Ostrand *et al.* 1998). Hunt (1995) speculated that murrelets attack schools and force them into small balls as they forage on them. However, this strategy may be less effective when the schools are larger and the feeding group size has not increased (Table 4) correspondingly. Greater depth to schools would require deeper foraging dives by murrelets, thereby increasing energy demands of obtaining forage (Burger 1991). Large herring may also have been difficult to capture, handle, or consume as suggested by their absence from murrelet diets (Burkett 1995). Collectively, these data suggest that the forage resources that were monitored in 1998 may have been energetically too expensive to pursue or were too large to be consumed. Murrelets may have selected resources that our survey did not detect. For example, Pacific Sandlance *Ammodytes hexapterus* appear to be underrepresented in our data set, with only four schools identified in three years. However, within PWS, during the time period of this study, about one half of the food items consumed by murrelets were sandlance (Kuletz, USFWS, Anchorage, Alaska, unpubl. data). Murrelets may have consumed more sandlance than our observations suggest, and they were observed foraging in waters closer to shore than our surveys covered (Kuletz, USFWS, Anchorage Alaska, unpubl. data). The 1998 data suggest that the prey available in our study area may have been energetically costly. Murrelets likely chose to forage elsewhere, where more preferable food items were available.

Our study of murrelet foraging and multi-year observations with other seabirds (Monaghan *et al.* 1994, Davoren 2000) have implications for resource selection modeling in general. Previous investigations (e.g. Ostrand *et al.* 1998, Maniscalco *et al.* 1998) modeled resource selection based on temporally-limited data. Such studies should be interpreted as indications of how animals select resources at a specific time and under specific environmental conditions. The range of selection patterns is likely to be broader than the results of these time-limited studies indicate. We also have not defined all murrelet forage selection models since we have not monitored the full range of possible environmental conditions. However, our findings suggest that foraging selection patterns varied as prey characteristics changed and that foraging theory had utility in predicting how murrelets adapted to those changes. As has been observed by others (Monaghan *et al.* 1994, Davoren 2000), this study illustrated the behavioral plasticity of seabirds living in highly variable environments.

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TABLE 5
Summary of logistic regression analysis, which compares fish schools associated with Marbled Murrelets to available schools. Analysis was conducted by year on data collected in Prince William Sound, Alaska

1997 Independent variables	Importance factor[1]	First AICc model[2]	1999 Independent variables	Importance factor[1]	First AICc model[2]
Intercept	1.00	−1.31	Intercept	1.00	−2.79
Area	0.52	−0.016	Herring	0.47	1.13
School depth	0.50	−0.024	Approx. backscatter	0.44	
Total water depth	0.36		Depth below school	0.40	
Depth below school	0.32		Distance to shore	0.39	
Herring	0.28		Gadids	0.37	
Approx. backscatter	0.28		Total water depth	0.38	
Distance to shore	0.27		School depth	0.30	
			Area	0.26	

[1]Importance value of independent variables based upon Akaike's information criterion corrected for small sample sizes (AICc) ranking of all possible models (see Burnham and Anderson 1998).

[2]Estimated coefficients for the best model based upon Akaike's information criterion corrected for small sample sizes (AICc) ranking of all possible models (see Burnham and Anderson 1998).

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