VARIATIONS IN THE DISTRIBUTIONS OF MARINE BIRDS WITH WATER MASS IN THE NORTHERN BERING SEA[1]

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Abstract. We examined the pelagic distributions of 12 species of northern Bering Sea birds with respect to the water masses in which they were observed during the summers of 1984, 1985 and 1986. Despite the prediction of earlier work that differences in community structure are unlikely to occur at small spatial scales, we found significant habitat preferences for all but one of the species studied. We suggest that the strength of the gradient between habitat types is the cause of this discrepancy, and that boundary conditions should also be considered when discussing the influence of spatial scales on community processes.

Key words: Seabird distributions; Bering Sea; habitat preferences; spatial scale; boundary conditions.

INTRODUCTION

Patterns in the distribution and abundance of seabirds at sea vary as a function of the spatial and temporal scales at which they occur (Hunt and Schneider 1987). According to these authors, macroscale (1,000–3,000 km; after Haury et al. 1978) patterns of seabird distribution most likely reflect variations in primary and secondary production, whereas mesoscale patterns (100–1,000 km) involve variations in avian species composition in response to variations in the composition of prey communities. At still smaller scales (1–100 km), the abundances of individual species often reflect opportunities to forage at local concentrations of prey (Hunt and Schneider 1987). In this generalized scheme, variations in the avian community are alternately characterized by changes in either biomass or species composition, and reflect a similar alternation in the prey community.

Despite the prediction, based on the above scheme, that differences in the species composition of seabird communities are unlikely to exist over relatively small spatial scales, at least two lines of evidence have indicated that such patterns exist. First, Haney (1986) has shown significant differences in the densities of several bird species over four water masses associated with Gulf Stream eddies while working at the

lower end of the mesoscale range (50–150 km). Second, in the Chirikov Basin of the northern Bering Sea, where three separate water masses occur in close proximity, investigations of the distribution of nesting colonies of marine birds have shown that colonies located in Alaska Coastal Water support primarily piscivorous species, whereas colonies near Anadyr Water are dominated by planktivorous auklets (Sowls et al. 1978, Springer and Roseneau 1985). These patterns indicate that differences exist in the use of different water masses by different species (Springer et al. 1987). This supposition was strengthened by limited transect data (Drury et al. 1981; summarized by Hunt et al. 1981) that showed considerable differences in use of the eastern and western portions of the Chirikov Basin by birds.

This paper investigates the foraging distributions of seabirds in the Chirikov Basin with respect to water masses and their constituent prey communities. We test whether a variety of species show habitat specificity when several habitats occur over a small area (on the order of the birds' daily flight ranges). The study, however, was conducted at a spatial scale generally associated with responses to changes in local prey concentrations (Schneider 1982, Schneider and Piatt 1986, Schneider et al. 1987), rather than to different prey communities. In addition to our findings for the Chirikov Basin, we discuss the effect of the boundary gradient between habitat patches on a bird's ability to respond to habitat changes and the need to examine the combined effects of boundary conditions and scale on habitat selection by birds.

METHODS

STUDY AREA

The Chirikov Basin lies between Siberia and Alaska and is bounded by St. Lawrence Island to the south and Bering Strait to the north (Fig. 1). The oceanography of the area is influenced by three water masses: to the east flows Alaska Coastal Water, to the west Anadyr Water, and between lies Bering Shelf Water (Coachman et al. 1975). These three water masses are distinct both in their physical and biological properties and can be readily distinguished by their salinity characteristics (Coachman et al. 1975).

Alaska Coastal Water originates from the Inner Domain of the southeastern Bering Sea shelf and moves northward along the coast, where it is diluted by extensive freshwater input in Norton Sound, primarily from the Yukon River (Coachman et al. 1975, Kinder and Schumacher 1981). This is the warmest of the three water masses. To the west is the colder, more saline Anadyr Water that enters from the Gulf of Anadyr, where the endemic cold water mixes with water flowing in from the southern Bering Sea (Coachman et al. 1975). The third water mass, Bering Shelf Water, is characterized by temperatures and salinities intermediate between those of Alaska Coastal Water and Anadyr Water, and by extensive stratification in summer (Coachman et al. 1975, Hunt and Harrison 1990). This water mass enters the Chirikov Basin around both ends of St. Lawrence Island and is formed by the mixing of cold water from the northern Bering Sea shelf and oceanic water from the Bering Sea (Coachman et al. 1975).

DATA COLLECTION AND ANALYSIS

Distributions of seabird species were determined using data collected over the periods 1–7 July 1984, 26 July–13 August 1985, and 11–21 August 1986, when numerous ship transects were made near St. Lawrence and King Islands (Fig. 2). For 1984, our data comes only from transects near King Island; during 1985 and 1986, the surveys covered much of the southern Chirikov Basin. Data collection along these transects entailed identifying, counting, and recording the behavior of all birds seen within a 300 m arc from directly in front, to 90° to the side, of the ship. This method is suitable for obtaining estimates of birds on the water, but tends to overestimate densities of flying birds (Tasker et al. 1984). The time of

each flock sighting was recorded to the nearest 0.1 min, and details of the ship's position and speed were noted at regular intervals to facilitate the calculation of bird densities. (For details of the methodology see Hunt and Harrison 1990, Hunt et al. 1990a.)

In the analysis, we divided transects, which varied in length and often traversed water mass boundaries, into 15-min (2.3–5.6 km long, depending on ship speed) intervals. For each interval, we calculated the position of the central point, the area over which birds were recorded, and the number of birds of each species seen during that period. To reduce data loss, intervals of 12.5–17.5 min from the ends of transects were included as samples. In the analysis, we ignored rarely encountered species and combined counts for all "dark-bellied shearwaters" [primarily Short-tailed (*Puffinus tenuirostris*), but including some Sooty Shearwaters (*P. griseus*)] and murres (*Uria* spp.) because there were high proportions of unidentified individuals for these taxa. For the 1985 data, however, separate tests were possible for each murre species because a high proportion (42.8%) of those seen were identified to species. The shearwater data from 1984 and 1985 were not analyzed because few were seen in either year. For Red Phalaropes (*Phalaropus fulicaria*) and the alcids we excluded from the analysis individuals that were first observed in flight. Because these species feed only from the water surface, this allowed us to exclude birds that were just flying to or from a feeding site. In all instances, numbers of birds were converted into densities (birds/km²) to allow comparisons between transect intervals covered at different speeds.

Distribution maps were created by dividing the region into blocks with dimension of 0.1 degrees of latitude and 0.2 degrees of longitude. This choice of block size was a compromise between obtaining a fine-grain resolution in the geographical distribution of birds and the sample size available for most blocks; with this block size, 48%, 46%, and 33% of the blocks had at least four counts in 1984, 1985, and 1986, respectively. For each block, we calculated the mean density of each species for all 15-min samples whose midpoint fell within that block.

The positions of the boundaries between water masses were determined using salinity (Coachman et al. 1975). In 1985 and 1986, Bering Shelf Water was defined as 31.8–32.5 ppt (Coachman 1986, Walsh et al. 1989), with Anadyr Water
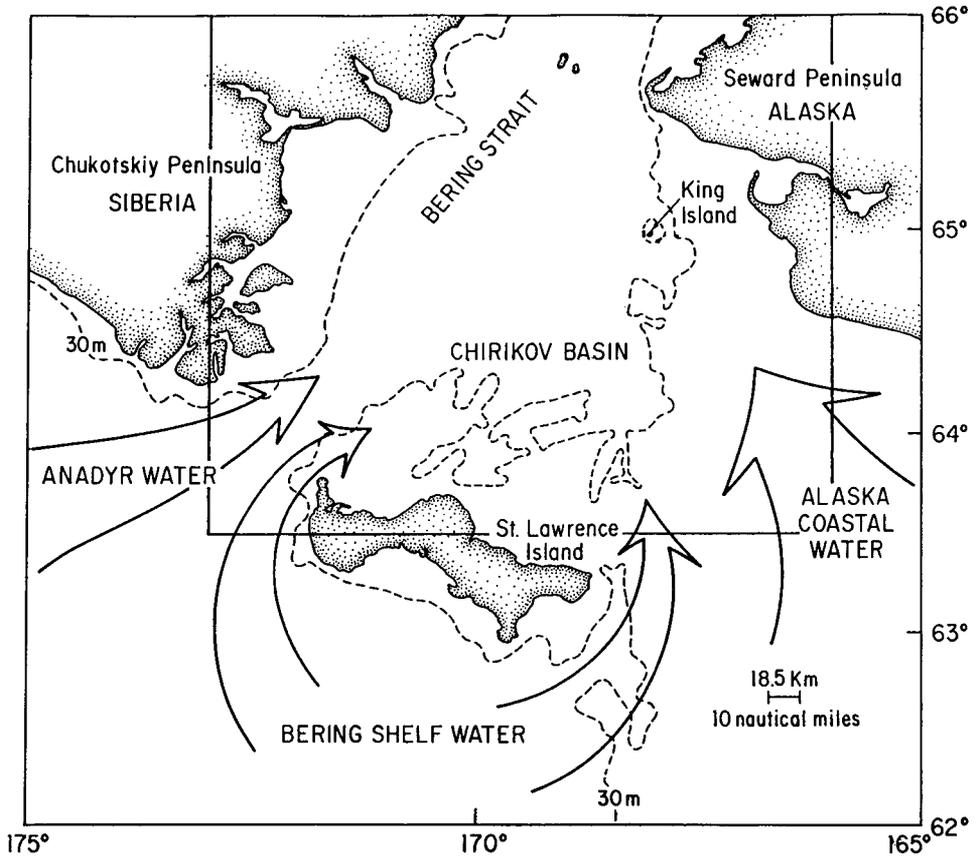
FIGURE 1.   Study area, showing generalized movements and origins of the major water masses flowing north through Bering Strait. Inner box shows area covered by distribution maps.

more saline, and Alaska Coastal Water less so. Although variations occur in the salinities of these water masses, they are typically small on a year to year time-scale (Coachman et al. 1975, Coachman and Shigaev, in prep.); hence, the same definitions were applied to the 1984 data. For 1985 and 1986, the locations of boundaries between water masses follow Coachman (1986:fig. 5; reproduced in part by Walsh et al. 1989), who produced maps based on extensive water sampling for the periods directly before and after the bird surveys. In addition, physical oceanographic data collected during bird surveys were used to determine more precisely the positions of water mass boundaries (see salinity profiles in Hunt and Harrison 1990 and Hunt et al. 1990a). Less-detailed information is available for 1984, although the position of the front between Alaska Coastal Water and Bering Shelf Water in the vicinity of King Island was determined by Hunt and Harrison (1990).

We then determined the water mass in which each 15-min interval was obtained. In cases where an interval intersected a boundary between water masses, the water mass over which its central point lay was taken to be that of the sample. This method of assigning samples to water masses is problematic in that it uses "average" positions for boundaries that fluctuate over time spans as short as a few days (Coachman 1986, Hunt and Harrison 1990). Misclassifications, however, are most likely to reduce, or have no affect on, the apparent significance of differences in bird densities in each water mass. Consequently, the P-values obtained are probably conservative.

During 1984 and 1986, data were collected in only two of the three water masses (Fig. 2); hence, for these years, we used Mann-Whitney U-tests
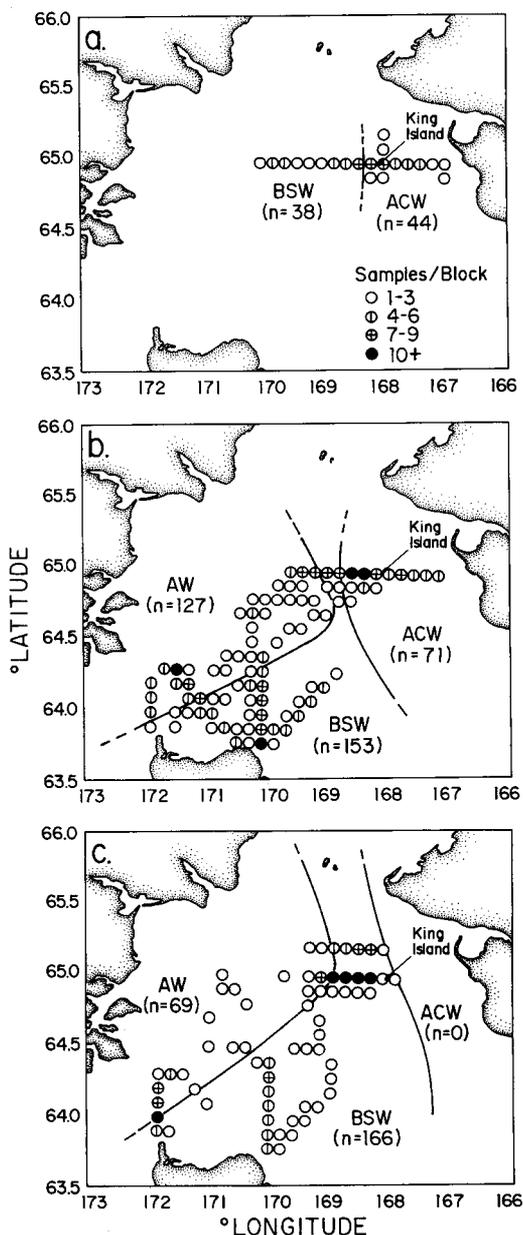
FIGURE 2. Water mass coverage for each of the three years of the study: a) 1984, b) 1985, c) 1986. AW = Anadyr Water; BSW = Bering Shelf Water; ACW = Alaska Coastal Water.

(Zar 1984) to determine whether a bird species occurred in each of the water masses equally. In 1985, all three water bodies were sampled, so we used Kruskal-Wallis tests to determine differences in habitat use. For those species that showed

a significant relationship, we used Dunn's multiple comparison test for nonparametric data of unequal sample sizes (Zar 1984). This test determines which differences in water mass use contribute to the significant result. In each case, a null hypothesis of no difference in use of the water masses was assumed.

Because these tests assume that samples are independent, we tested for autocorrelation within the data set. These tests were conducted for each species on each transect and yielded 35 (8.3%) out of 422 tests in which the lag-1 coefficient lay outside the critical region and the null hypothesis of independence could not be accepted. Even with independent samples, however, one would expect 1 out of every 20 tests (5.0%) to produce a value that lies outside this region (Chatfield 1980). Consequently, we chose not to reject data from nine cases that had coefficients that were only just outside the critical region. The data from the remaining 26 cases with significant coefficients of autocorrelation were not used in the analysis. Tests were carried out using SYSTAT (Wilkinson 1990) and employed a significance level of 5%.

RESULTS

Significant relationships between bird distributions and water masses were detected, in at least one year, for each of the species considered except for the separate analysis for Thick-billed Murres (*Uria lomvia*) in 1985 (Table 1). These relationships varied in their extent and nature between species and in a few cases between years for the same species. Further, the types of relationships differed between species that are predominantly planktivorous and those that are piscivorous.

PLANKTIVOROUS BIRDS

The planktivorous species [shearwaters, Red Phalarope, Least (*Aethia pusilla*) and Crested (*A. cristatella*) auklets], and the omnivorous Northern Fulmar (*Fulmarus glacialis*), occurred in higher densities in Bering Shelf and Anadyr Water than in Alaska Coastal Water (Fig. 3, Tables 1, 2). Within this group, further differences existed between species with different feeding strategies. The procellarids showed consistent preferences for the most westerly water mass sampled (i.e., that with the strongest Anadyr Water influence; Figs. 4a, b). Red Phalaropes showed a strong preference for Anadyr Water in 1985, but they

TABLE 1.   Results of statistical comparisons of use of water masses by species commonly found in the Chirikov Basin. The Mann-Whitney U-statistic is given for 1984 and 1986, and the Kruskal-Wallis H-statistic is given for 1985. Values in parentheses are sample sizes for AW, BSW, and ACW, respectively. Sample sizes vary among species, within years, due to the need to exclude transects with excessive levels of autocorrelation between samples.

| | Year | | | | | |
| | 1984 | | 1985 | | 1986 | |
Species	U	P	H	P	U	P
Northern Fulmar	193.5	<0.001	111.1	<0.001	3,911.5	0.009
	(−, 21, 41)		(119, 124, 71)		(67, 149, −)	
'Dark-bellied' Shearwater	−		−		4,499.0	0.009
					(69, 166, −)	
Black-legged Kittiwake	941.5	0.325	26.3	<0.001	5,255.5	0.196
	(−, 38, 44)		(104, 144, 40)		(64, 148, −)	
Red Phalarope	616.0	<0.001	12.6	0.002	5,456.5	0.086
	(−, 38, 44)		(106, 139, 65)		(69, 166, −)	
Parakeet Auklet	575.0	0.014	7.5	0.024	5,135.5	0.145
	(−, 38, 44)		(117, 148, 46)		(69, 166, −)	
Least Auklet	166.0	<0.001	86.6	<0.001	1,804.5	<0.001
	(−, 38, 44)		(114, 118, 34)		(53, 116, −)	
Crested Auklet	627.5	0.004	59.5	<0.001	5,041.5	0.900
	(−, 38, 44)		(127, 143, 71)		(67, 149, −)	
All murres	1,327.5	<0.001	3.9	0.142	5,461.0	0.263
	(−, 38, 44)		(118, 123, 59)		(67, 149, −)	
Common Murre	−		5.8	0.056	−	
			(118, 147, 59)			
Thick-billed Murre	−		2.1	0.355	−	
			(116, 104, 59)			
Horned Puffin	1,135.5	<0.001	27.1	<0.001	5,417.5	0.187
	(−, 38, 44)		(127, 153, 71)		(69, 166, −)	
Tufted Puffin	1,312.0	<0.001	7.9	0.020	5,955.0	0.386
	(−, 38, 44)		(127, 153, 71)		(69, 166, −)	

did not in 1986 (Fig. 3, Tables 1, 2). In all years, however, phalaropes were most numerous in areas where Gray Whales (*Eschrichtius robustus*) were seen (Fig. 4c; also see Obst and Hunt 1990). The two *Aethia* auklets occurred in highest densities in Bering Shelf Water in 1984 and 1985 (Fig. 3). In 1986, Least Auklets apparently favored Anadyr Water (Fig. 3, Table 1). Inspection of Fig. 4d, however, also shows high densities in stratified Bering Shelf Water north of St. Lawrence Island and near the front to the west of King Island. No preference for any water mass was detected for Crested Auklets in 1986. Parakeet Auklets occurred in highest densities in Bering Shelf Water in 1984, avoided that water in 1985, and exhibited no preference in 1986.

PISCIVOROUS BIRDS

In contrast to the planktivores, those seabird species that forage primarily on fish [Black-legged Kittiwakes (*Rissa tridactyla*), murres, and puffins (*Fratercula* spp.)] either occurred at highest densities in Alaska Coastal Water or exhibited no preference for any water mass (Fig. 5, Tables 1, 2). In 1986, when coastal water was not sampled, none of these species showed a significant preference for either of the other water masses (Table 1). The comparison of the two murres' distributions during 1985 revealed differences in their pattern of habitat use. Although Kruskal-Wallis tests failed to show a significant preference for either species (Table 1), the result for Common Murres (*U. aalge*) was very close to the 0.05 level ($P = 0.056$). Consequently, we carried out a multiple comparison test for this species which showed significantly higher densities in Alaska Coastal Water, than in Bering Shelf Water, although not when compared with Anadyr Water (Table 2). This weak relationship is of interest given the absence of any differences between
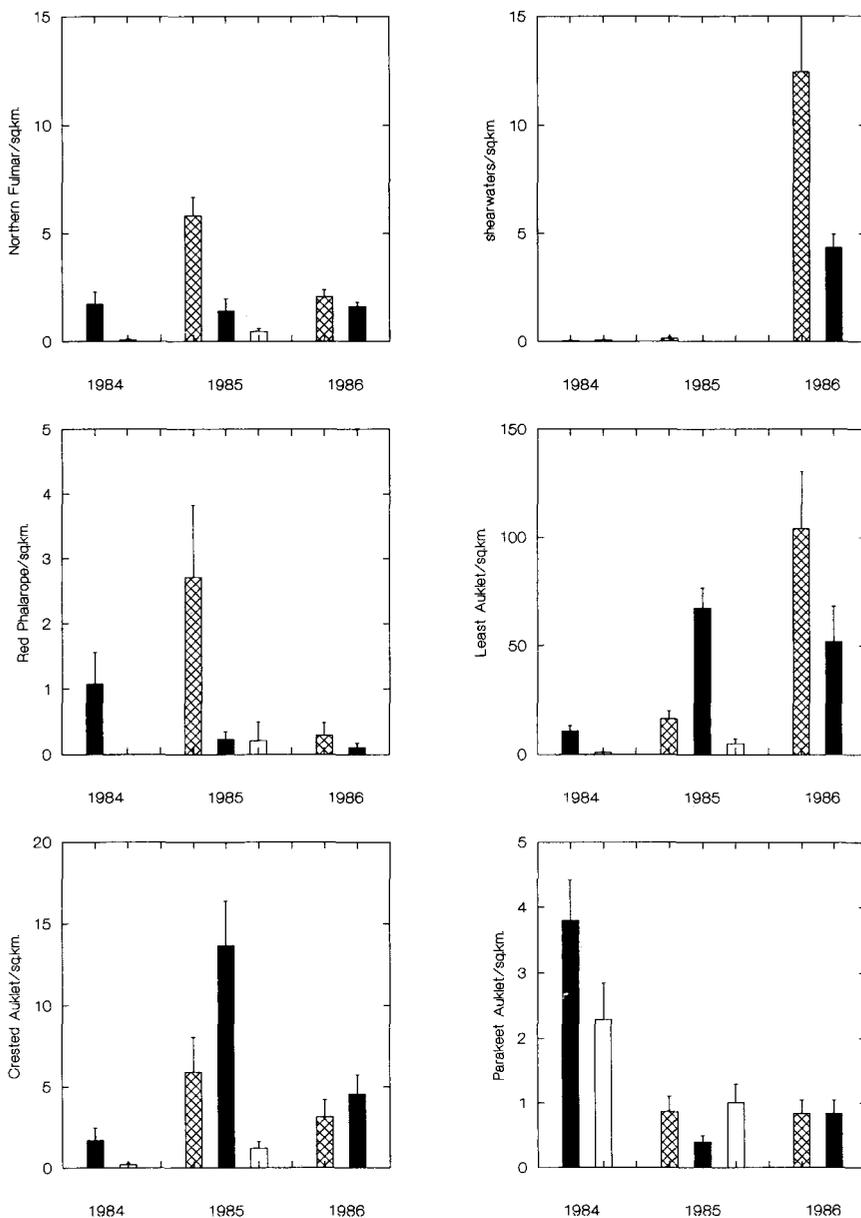
FIGURE 3.   Mean densities of planktivorous species in each water mass, for 1984–1986. Open bars = Alaska Coastal Water; solid bars = Bering Shelf Water; cross-hatched bars = Anadyr Water. Error bars give standard errors. Sample sizes are as given in Table 1.

water masses in the densities of Thick-billed Murres.

Horned (*Fratercula corniculata*) and Tufted (*F. cirrhata*) puffins both showed preferences for Alaska Coastal Water in the two years when it was sampled (Fig. 5, Tables 1, 2). The contrast

in the densities of puffins in each water mass was particularly striking in 1984 (Fig. 6). These two species often forage close to their colonies (Sealy 1973, Hunt et al. 1981) which creates the potential for a confounding effect of colony position within our analysis. If colony situation were hav-
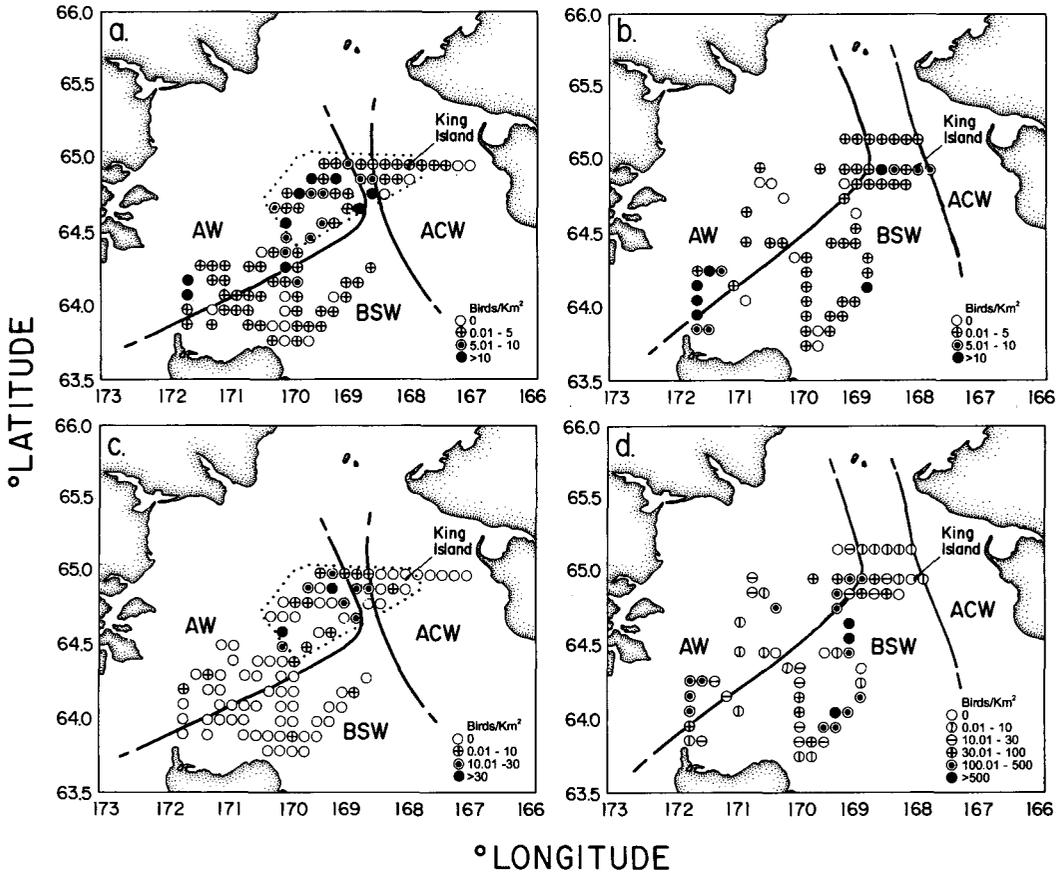
FIGURE 4. Pelagic distributions of some planktivorous species across the Chirikov Basin: a) Northern Fulmar, 1985; b) "dark-bellied shearwaters," 1986; c) Red Phalarope, 1985; d) Least Auklet, 1986. The polygon of small dots on a) and c) shows the region in which Gray Whales were commonly seen.

ing a primary influence on where puffins forage, then one would expect them to be equally distributed around their colonies. Inspection of the data, however, shows that their distribution extends much farther to the east of King Island than to the west, where their occurrence ends near the boundary between Alaska Coastal Water and Bering Shelf Water (Fig. 6).

DISCUSSION

Our results support the hypothesis that the pelagic distributions of seabirds across the Chirikov Basin reflect preferences for one or more of the three water masses, as predicted by Drury et al. (1981) and Springer et al. (1987). The variation in these preferences, however, indicates that factors other than water mass also have some influence. Preferences for water masses fell into two broad categories, with planktivorous bird species using Anadyr Water and Bering Shelf Water most frequently and piscivorous species primarily using Alaska Coastal Water. For some bird species, the boundaries between water masses appeared to set the limits of foraging distributions (e.g., puffins; Fig. 6), whereas for others the frontal areas were a focus of foraging activity [e.g., Least Auklets (Hunt and Harrison 1990) and shearwaters (Fig. 4b)].

The concentrations of shearwaters in Anadyr Water, and in particular near the front between Anadyr and Bering Shelf Waters (Fig. 4b), may reflect a dependence on frontal systems for the availability of prey. These shearwaters also concentrate near the Inner Front in the southeastern Bering Sea (Schneider 1982) and near a front to the north of St. Paul Island that is physically

TABLE 2.   Results of Dunn's multiple comparison tests between each pair of water masses for 1985. For each comparison, the water mass with the highest density of birds, and Q, are given. Significance levels: $* = P < 0.05$, $** = P < 0.01$, $*** = P < 0.001$.

| Species | Water mass preferred in the comparison of | | |
	AW/BSW	BSW/ACW	AW/ACW
Northern Fulmar	AW	BSW	AW
	8.65***	1.77	9.19
Black-legged Kittiwake	AW	ACW	ACW
	2.12	5.10***	3.43**
Red Phalarope	AW	ACW	AW
	3.06**	0.53	3.01**
Parakeet Auklet	AW	ACW	ACW
	1.85	2.51*	1.14
Least Auklet	BSW	BSW	AW
	7.57***	6.63***	3.42**
Crested Auklet	BSW	BSW	AW
	4.11***	7.62***	4.09***
Common Murre	AW	ACW	ACW
	0.79	2.41*	1.71
Horned Puffin	BSW	ACW	ACW
	0.62	4.55***	4.91***
Tufted Puffin	BSW	ACW	ACW
	2.80**	0.97	1.34
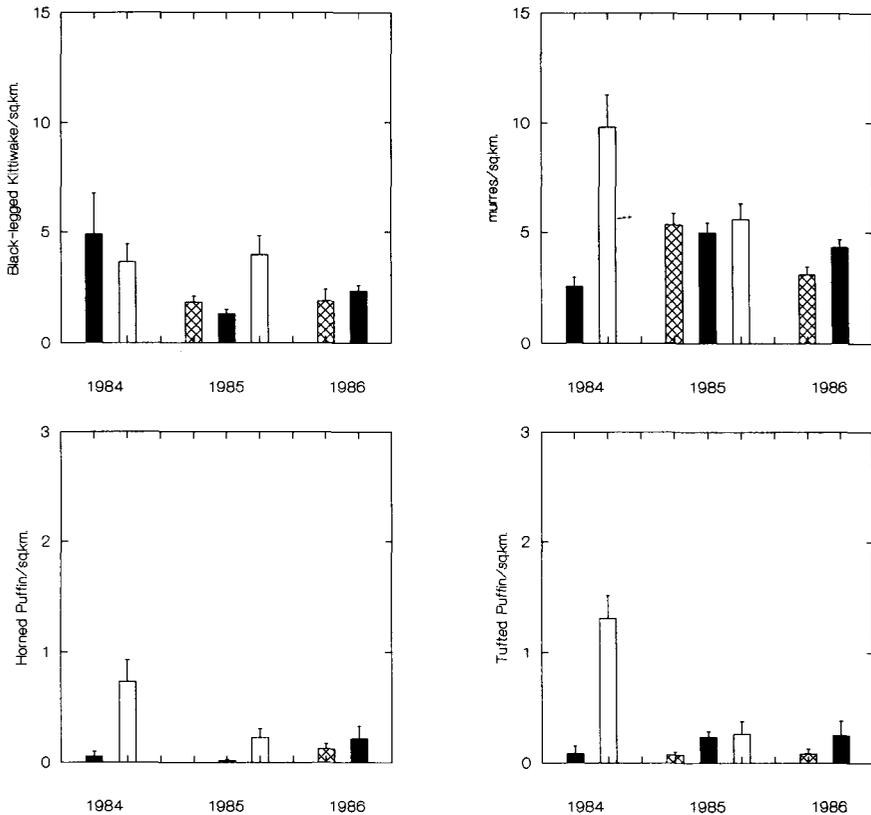
FIGURE 5.   Mean densities of piscivorous species in each water mass, for 1984–1986. Symbols as described for Figure 3.

equivalent to the Inner Front (Coyle and Cooney, in press). At this latter front, shearwaters forage on *Thysanoessa raschii* (Hunt et al., unpubl.). We do not know the diets of these shearwaters in the Chirikov Basin, but if they are taking euphausiids, the strong vertical fluxes associated with the edge of the Anadyr Current (Haney 1991) could aid in concentrating and transporting this prey upward in the water column.

During this study, Least Auklets were widespread in both Anadyr and Bering Shelf Waters. Other analyses have shown that within these water masses they tended to concentrate in frontal regions (Hunt and Harrison 1990, Harrison et al. 1990) and over stratified water (Hunt et al. 1990a, Hunt and Harrison 1990). These conclusions, based on the analysis of individual transects, are borne out by our Figure 4d which shows highest densities close to the front between Anadyr and Bering Shelf Waters and offshore to the north of St. Lawrence Island, where water tends to be well stratified (Hunt et al. 1990a; Coachman and Shigaev, in prep.). Inspection of the data from the earlier analyses showed that Least Auklets used stratified water only when Bering Shelf Water was present in the upper mixed layer (e.g., Hunt and Harrison 1990:fig. 8). When Alaska Coastal Water overlay Bering Shelf Water, Least Auklets were largely absent. This observation may explain the results of Haney (1991), who found that Least Auklets avoided strongly stratified water near shore at the western end of St. Lawrence Island. He did not identify the origin of this water or the composition of its plankton community, but if the upper mixed layer was derived from terrestrial runoff, the copepods that are the principal prey of Least Auklets may have been absent.

Our results for Crested Auklets indicate that, like Least Auklets, they prefer Bering Shelf Water, suggesting that they may also favor stratified water. In contrast, Parakeet Auklets exhibit no consistent preference for any water mass. This suggests that factors determining Parakeet Auklet distributions are independent of water mass and, hence, differ from those influencing the distribution of the other auklets (Harrison 1987).

Obst and Hunt (1990) showed that four of the species discussed here tend to associate with Gray Whales in the Chirikov Basin. Our analysis shows that two of these (Northern Fulmar and Red Phalarope) also showed a preference for Anadyr Water and that within this water mass they oc-
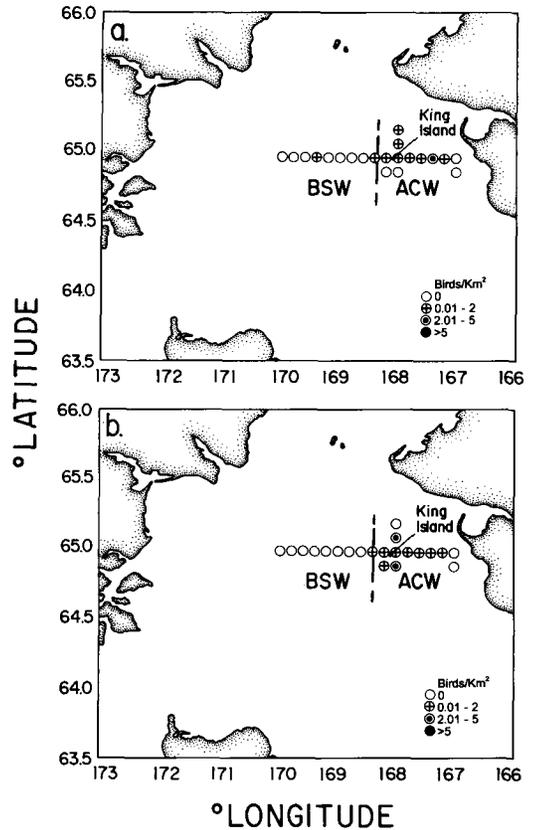
FIGURE 6.   Pelagic distributions of a) Horned and b) Tufted puffins around King Island in 1984.

curred in highest densities in the region where Gray Whales were most commonly seen (Figs. 4a, c). The other two species (Black-legged Kittiwake and Thick-billed Murre) did not exhibit similar water mass preferences, and in 1985 the former preferred Alaska Coastal Water, a preference similar to other piscivores. These differences suggest that whales act to concentrate avian predators once they have already chosen their foraging habitat, rather than being the primary attraction. As the area in which Gray Whales were most frequently seen during this study extends across all three water masses (Fig. 7), one might therefore expect different assemblages of birds associating with whales in each water mass.

The preference of largely planktivorous species for Bering Shelf Water and Anadyr Water is understandable because of the presence of larger prey species (e.g., *Neocalanus plumchrus, N. cristatus* and *Eucalanus bungii*) there (Springer et al.
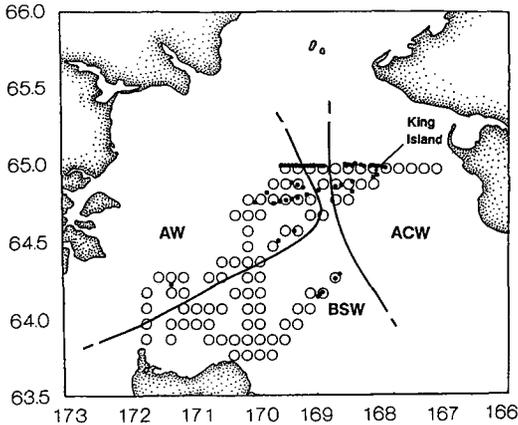
FIGURE 7. Distribution of Gray Whales in the Chirikov Basin in 1985. Filled circles represent sightings of at least one individual; open circles represent blocks through which transects were made.

1989, Hunt and Harrison 1990, Hunt et al. 1990a). These prey are not numerous in Alaska Coastal Water, and are presumed to be sufficiently more profitable as food items than the more numerous small zooplankton. In contrast, we do not know why piscivores apparently avoid Bering Shelf Water and Anadyr Water, but little is known about the abundance of fish species in the different water masses. Some of the region's most important species of forage fish [e.g., sandlance (*Ammodytes hexapterus*), capelin (*Mallotus villosus*); Drury et al. 1981, Springer et al. 1987] spawn in shallow water or the intertidal zone (Hart 1973) and are therefore at least periodically abundant in coastal waters. Much of the Alaska Coastal Water is more than 90 km from shore, however, and there are no data of which we are aware on the abundance of forage fish in offshore areas. Based on the distributions of the piscivorous seabird species, we can only hypothesize that fishes must be more available in Alaska Coastal Water than in the other water masses of the Chirikov Basin.

An alternative explanation for the preference of the piscivores for Alaska Coastal Water is that they prefer to forage in shallow water. Haney (1991) found that large alcids near the western end of St. Lawrence Island occurred in higher numbers in shallower water. He hypothesized that these birds may take a large proportion of epibenthic fish in their diets and that foraging in shallow water would be more efficient energeti-

cally. This argument, however, would not explain the preference of surface-feeding kittiwakes for Alaska Coastal Water. To test the validity of Haney's argument for the piscivorous alcids, we will have to learn the distribution by depth and water mass of the prey species identified by Springer et al. (1987).

Recently, both marine (e.g., Steele 1978, 1989; Schneider and Duffy 1985) and terrestrial (e.g., Wiens 1976) ecologists have focused on the importance of the scale of habitat heterogeneity for ecological processes. An underlying concept is that there may be characteristic spatial (and temporal) scales at which certain processes occur (e.g., Haury et al. 1978, Steele 1978, Hunt and Schneider 1987). Throughout these discussions the spatial scales associated with different processes are explicitly addressed. The biological importance of the boundary conditions that define habitat regions, however, have seldom been described. Kotliar and Wiens (1990) have recently proposed that the nature of patch boundaries may change with patch size; large-scale patches may have more ambiguous bounds than small patches. They also emphasized a continuum in the degree of contrast between a patch and the matrix in which it exists. We suggest that the degree of contrast is not necessarily a function of the scale of the patch but may be independent of patch size. We hypothesize that a predator's ability to recognize a habitat patch will depend on both the size of the patch, and the sharpness of its contrast with the surrounding matrix. For example, the differences in seabird species distributions described for the Chirikov Basin were detectable over the small scales at which one might have expected to find differences in the biomass of avian predators, but not in species composition (Hunt and Schneider 1987). We suggest that this segregation of habitat use depended on the strong fronts (steep property gradients) bounding the three water masses that created sharp gradients in the distribution and abundance of prey to which the predators responded (Hunt and Harrison 1990). Had these gradients been weaker, one would expect that the dramatic differences in use of water masses over short distances west of King Island would have been much reduced or absent. Other evidence from marine birds suggests that at scales below the mesoscale, birds largely ignore weakly defined habitats (e.g., Hunt et al. 1990b), whereas when definition is strong, habitat patches are used

differentially (e.g., Haney 1986, Hunt and Harrison 1990, Veit and Hunt 1991). In contrast, at mesoscales and above, even weakly-defined habitats differ in use (e.g., Schneider et al. 1986, Hunt and Schneider 1987, Hunt et al. 1990b). Thus, the scheme described by Hunt and Schneider (1987) may need modification. It may not be possible to characterize the types of relationships between seabirds and their prey solely by spatial scale, but rather by a combination of both the scale and the strength of the boundaries that define a habitat type.

ACKNOWLEDGMENTS

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