suses (Census Periods 2–5). Use of the four types of plots sampled differed markedly among the study species (Table 5). Differences in habitat use were statistically verified for five species—Semipalmated Sandpiper, Pectoral Sandpiper, Dunlin, Red Phalarope, and Lapland Longspur (Table 6, Fig. 5). Dry plots were little used by any of the study species during the breeding season, and this was a major contributing factor to the differences in habitat use of the five species exhibiting statistical differences in use of plot types.

There was, however, evidence of attraction to some plot types. Dunlin appeared to make disproportionately high used of the PMRA, and Lapland Longspur density was much higher on nonsaline plots than any other plot type (Table 5). In general, the most diverse area for birds during the breeding-season was the PMRA, where six of the ten study species reached their highest abundance. Nonsaline plots appear to have the highest use by birds, due to the high densities of Semipalmated Sandpiper and Lapland Longspur.

Brood-Rearing Season

The brood-rearing-period analyses are based on the average densities recorded on plots during Census Periods 8–10 (19 July through 9 August). Difference among plot types (Table 7) was much less pronounced than during the breeding season. Only two species—Semipalmated and Pectoral sandpipers—exhibited statistically significant differences among plot types (Table 8, Fig. 6). Both species made very low use of dry plots, and Pectoral Sandpiper appeared to make disproportionately high use of the PMRA during this portion of the summer.

During the breeding season, the PMRA had the highest bird diversity, with more species peaking in abundance in that area than any other plot type. This was not the situation during the brood-rearing period, when a few species peaked in each habitat type. The only tendency for a general trend was that most species had their lowest density in dry plots; however, Buff-breasted Sandpiper and Lapland Longspur were exceptions in appearing to favor dry plots.

Post-Breeding Season

The post-breeding season is defined as Census Periods 6 and 7 (10–23 August). Habitat use during this period was markedly different from earlier portions of the summer (Table 9). Pectoral Sandpiper, Buff-breasted Sandpiper, Red Phalarope, and Lapland Longspur exhibited statistically significant difference in use of the four types of plots (Table 10, Fig. 7), but all had different patterns of habitat use. Pectoral Sandpiper made high use of the PMRA but low use of dry plots. Buff-breasted Sandpiper demonstrates the opposite pattern. This species was most common in dry plots; none was found in the PMRA. Both Red Phalarope and Lapland Longspur appeared to prefer the saline plots. Red Phalarope did not occur on dry plots, and Lapland Longspur made relatively little use of the PMRA.

Overall, saline plots were the most widely used plot type during the post-breeding season. Half of the species occurred in their highest densities in this type. Dry plots continued to be little used by most species; however, densities of Lesser Golden-Plover and Buff-breasted Sandpiper were much higher in dry plots than any other habitat type.

Gradients

Nest Density

Geographic gradients were found for nest densities of six of the ten study species (Table 11). Distance from coast was a determinant of density for five of these species: Dunlin, Stilt Sandpiper, Red-necked Phalarope, Red Phalarope, and Lapland Longspur. The sixth species, Buff-breasted Sandpiper, exhibited density trends along an east-west geographic axis. Coastal influences were most important (primary variable in regression results) for Stilt Sandpiper, Red Phalarope, and Lapland Longspur (Fig. 8). Red Phalarope density decreased at inland locations, whereas the other two species increased inland from the coast.

These results are important in that they reveal the presence of two gradients operating over relatively short distances that exert rather pronounced influences on nest densities. In the case of Dunlin, Stilt Sandpiper, and Red-necked Phalarope, 10 to 15 percent of the variability in nest densities appears to be attributable to these gradients.

Breeding-Season Density

Geographic gradients were important in describing abundance trends of eight of the study species during the breeding season (Table 12). Only Lesser Golden-Plover and Pectoral Sandpiper abundances were relatively unaffected by coastal and east-west gradients. These factors were especially important predictors of abundance of Stilt Sandpiper, Dunlin, and Lapland Longspur; for these species, 10 to 30 percent of the variability of densities is attributable to plot lo-

Table 7. Average brood-rearing-season density (#/km²) of birds in coastal habitats and the PMRA.

Species	PMRA	Saline	Nonsaline	Dry
King Eider	3.3	4.0	8.0	0.0
Lesser Golden-Plover	8.7	15.7	8.7	7.3
Semipalmated Sandpiper	14.0	14.3	7.7	2.7
Pectoral Sandpiper	26.7	15.3	13.7	0.3
Dunlin	5.3	4.0	3.3	1.0
Stilt Sandpiper	0.0	2.0	2.7	0.0
Buff-breasted Sandpiper	0.7	0.0	0.7	1.3
Red-necked Phalarope	5.7	13.3	10.0	2.7
Red Phalarope	5.7	2.7	4.7	0.0
Lapland Longspur	11.0	28.7	27.3	34.7

Table 8. Test results of Kruskal-Wallis analyses for among-year changes in brood-rearing season bird density (d.f. = 3). "H" is the Kruskal-Wallis test statistic.

Species	H	p	Comments
King Eider	3.239	0.3563	
Lesser Golden-Plover	0.837	0.8407	
Semipalmated Sandpiper	7.832	**0.0496**	Low use of dry
Pectoral Sandpiper	15.239	**0.0016**	Low use of dry, high use of PMRA
Dunlin	4.82	0.1855	
Stilt Sandpiper	1.672	0.6433	
Buff-breasted Sandpiper	0.896	0.8265	
Red-necked Phalarope	7.623	0.0545	
Red Phalarope	6.407	0.0934	
Lapland Longspur	5.34	0.1485	

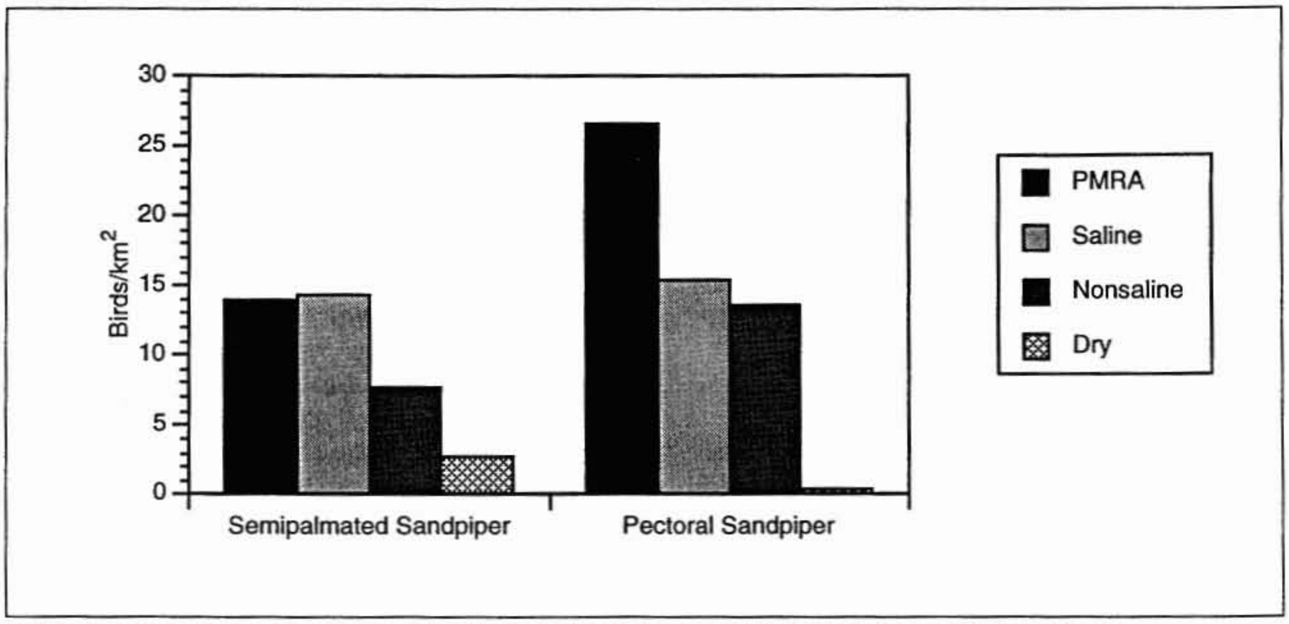

Figure 6. Brood-rearing-season densities of the species having significant differences among plot types.

Table 9. Average post-breeding-season density (#/km²) in coastal habitats and in the PMRA.

Species	PMRA	Saline	Nonsaline	Dry
King Eider	1.5	0.0	0.0	0.0
Lesser Golden-Plover	4.0	6.5	6.0	27.5
Semipalmated Sandpiper	0.5	2.1	4.5	0.0
Pectoral Sandpiper	55.5	14.5	24.5	2.5
Dunlin	5.5	25.0	10.5	3.5
Stilt Sandpiper	4.5	6.0	1.5	0.0
Buff-breasted Sandpiper	0.0	10.0	4.0	22.0
Red-necked Phalarope	12.5	38.0	3.5	1.0
Red Phalarope	6.5	12.5	6.5	0.0
Lapland Longspur	10.5	92.0	37.5	43.0

Table 10. Test results of Kruskal-Wallis analyses for among-area differences in post-breeding-season bird density.

Species	H	p	Comments
King Eider	0.22	0.9744	
Lesser Golden-Plover	4.127	0.2481	
Semipalmated Sandpiper	7.386	0.0606	
Pectoral Sandpiper	14.29	**0.0025**	High use of PMRA
Dunlin	6.766	0.0798	
Stilt Sandpiper	1.38	0.7102	
Buff-breasted Sandpiper	11.818	**0.008**	High use of dry
Red-necked Phalarope	2.375	0.4983	
Red Phalarope	9.765	**0.0207**	High use of saline; low use of dry
Lapland Longspur	13.25	**0.0041**	High use of saline; low use of PMRA

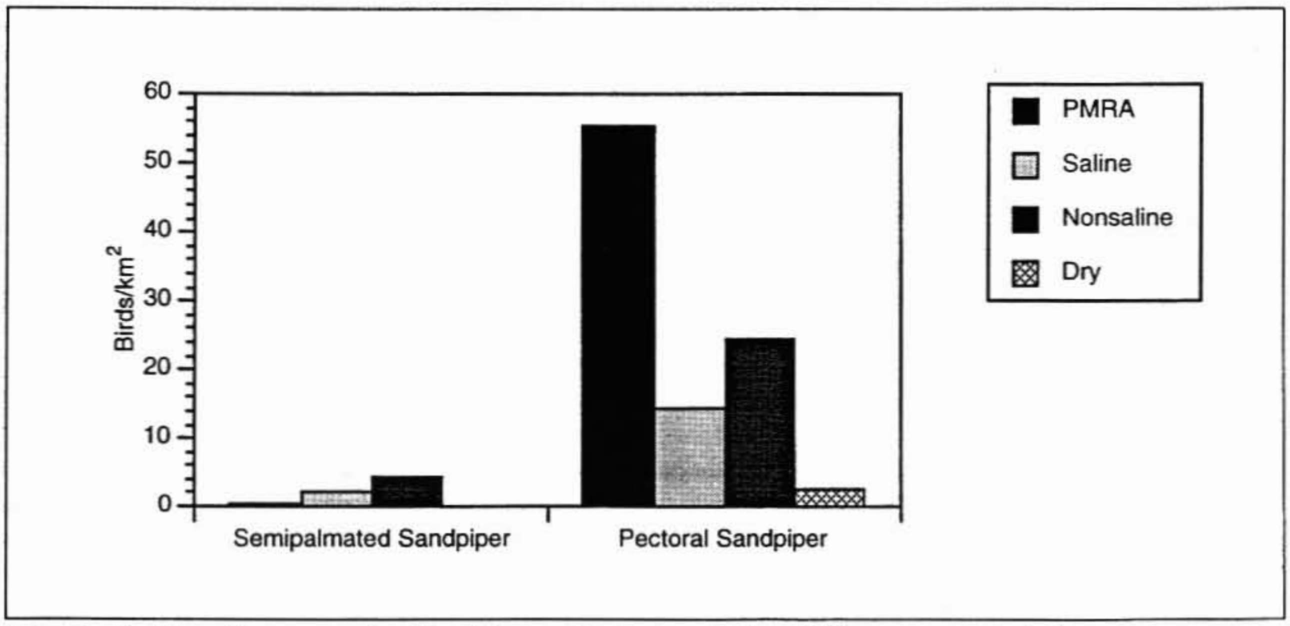

Figure 7. Post-breeding-season densities of the species having significant differences among plot types.

Table 11. Results of stepwise regression analyses of nest density in relation to distance from the coast and along an east-west gradient (total d.f. = 209). The order (relative importance) that the distance from the coast or along the east-west gradient is listed if these variables participated in the regression model. If no entry is made, neither variable exhibited a demonstrable relationship with nest density.

Species	F	Coast	East	r^2	Increasing Density
King Eider					
Lesser Golden-Plover					
Semipalmated Sandpiper					
Pectoral Sandpiper					
Dunlin	17.275	2	1	0.143	West and coastal
Stilt Sandpiper	10.737	1	2	0.094	Inland and west
Buff-breasted Sandpiper	5.111		1	0.024	West
Red-necked Phalarope	18.706	2	1	0.153	East and inland
Red Phalarope	4.679	1		0.022	Coastal
Lapland Longspur	4.489	1		0.021	Inland

Table 12. Results of stepwise regression analyses of breeding-season densities in relation to distance from coast and along an east-west gradient (total d.f. = 209). The order (relative importance) that the distance from the coast or along the east-west gradient is listed if these variables participated in the regression model. If no entry is made, neither variable exhibited a demonstrable relationship with bird density.

Species	F	Coast	East	r^2	Increasing Density
King Eider	5.921	1	2	0.054	Coastal and west
Lesser Golden-Plover					
Semipalmated Sandpiper	5.171	1		0.024	Inland
Pectoral Sandpiper					
Dunlin	30.437	2	1	0.227	West and coastal
Stilt Sandpiper	47.526	1	2	0.315	Inland and west
Buff-breasted Sandpiper	4.128		1	0.019	West
Red-necked Phalarope	5.364	2	1	0.049	East and inland
Red Phalarope	5.987	1	2	0.055	Coastal and west
Lapland Longspur	26.664		1	0.114	West

cation. The species most affected by distance from coast were King Eider, Semipalmated Sandpiper, Stilt Sandpiper, and Red Phalarope. Distance from the coast was also important in affecting densities of Dunlin and Red-necked Phalaropes but was secondary to location on an east-west axis.

Trends in abundance of some species whose abundance appears to be most affected by distance from the coast—Stilt Sandpiper, Dunlin, and Red Phalarope—are shown in Figure 9. Stilt Sandpiper increase in abundance inland, whereas both Dunlin and Red Phalarope were found in higher densities on plots near the coast.

Post-Breeding-Season Density

Geographic location was important in determining densities for six of the ten study species during the post-breeding season (Table 13), describing up to 20 percent of the among-plot variability in density. Four of these species—Semipalmated Sandpiper, Dunlin, Red Phalarope, and Lapland Longspur—exhibited density gradients in relation to distance from the coast. Except for Lapland Longspur, all these coastal gradients involved higher densities in proximity to the coast. Trends of the species exhibiting the strongest coastal gradients are illustrated in Figure 10.

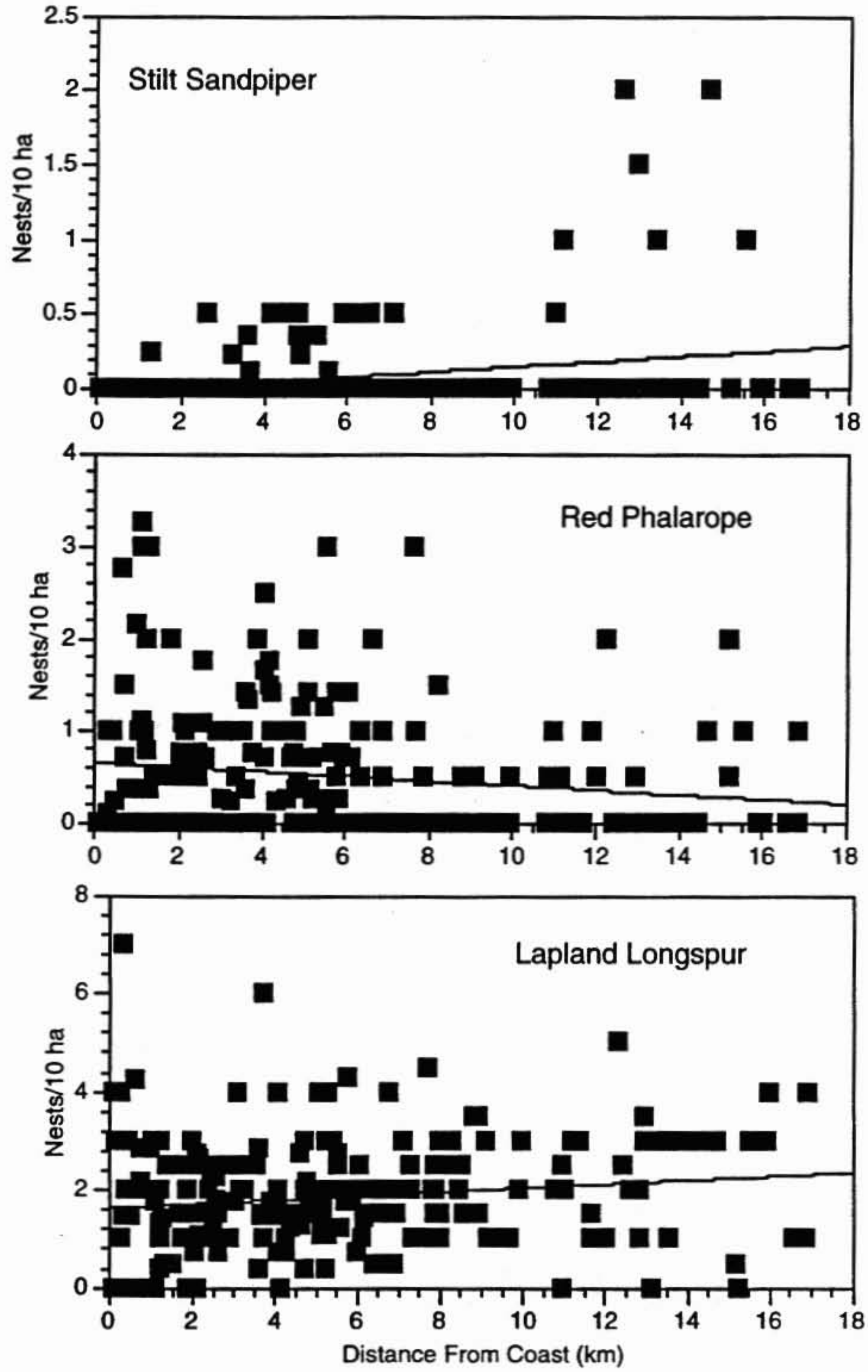

Figure 8. Trends in nest densities in relation to distance from coast of Stilt Sandpiper, Red Phalarope and Lapland Longspur.

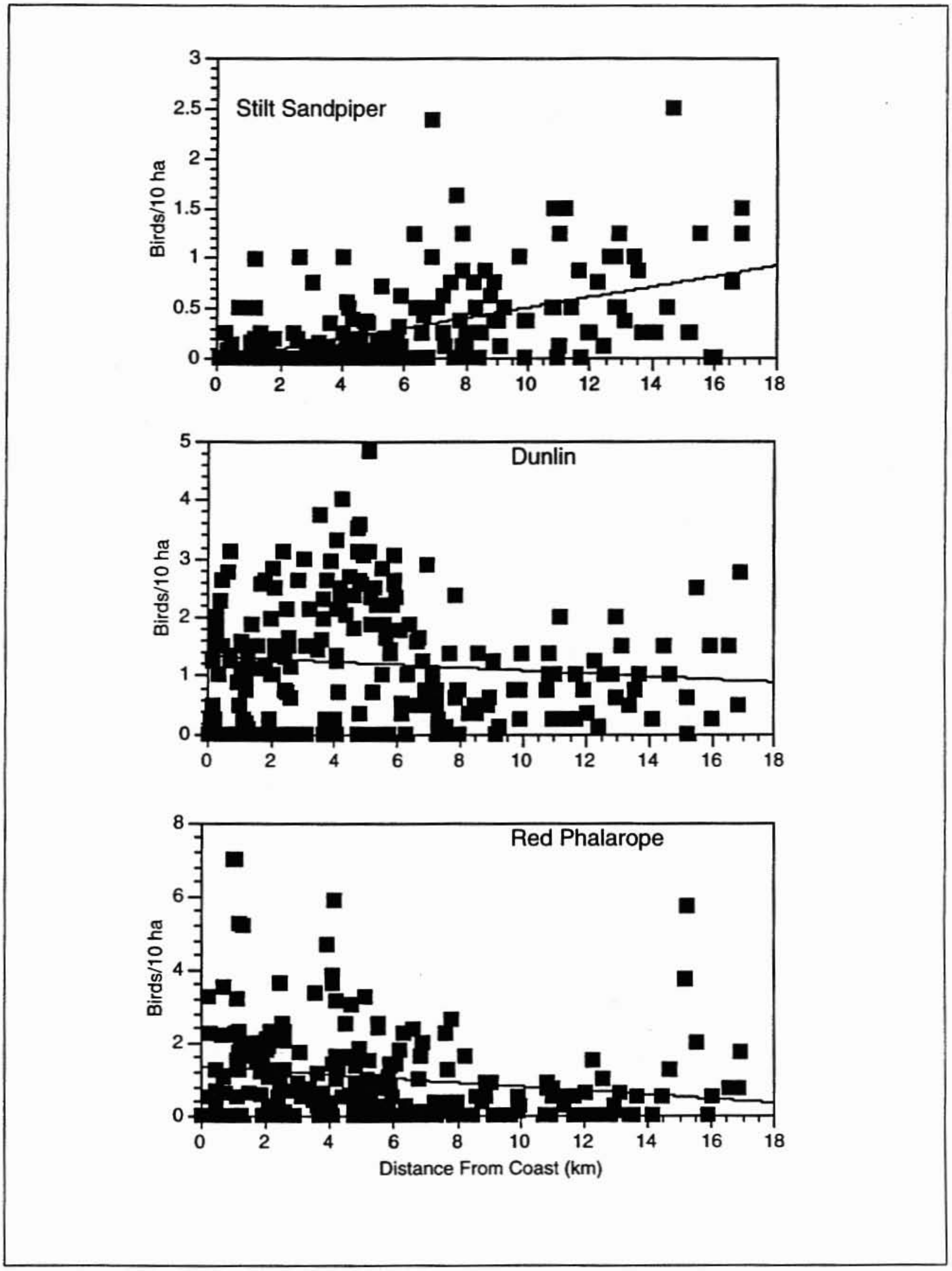

Figure 9. Trends in breeding-season densities in relation to distance from coast of Stilt Sandpiper, Dunlin, and Red Phalarope.

Table 13. Results of stepwise regression analyses of post-breeding-season densities in relation to distance from coast and along an east-west gradient (total d.f. = 180). The order (relative importance) that the distance from the coast or along the east-west gradient is listed if these variables participated in the regression model. If no entry is made, neither variable exhibited a demonstrable relationship with bird density.

Species	F	Coast	East	r^2	Increasing Density
King Eider					
Lesser Golden-Plover	16.487		1	0.084	East
Semipalmated Sandpiper	10.491	1	2	0.105	Coastal and west
Pectoral Sandpiper					
Dunlin	6.166	1	2	0.065	Coastal and west
Stilt Sandpiper					
Buff-breasted Sandpiper	23.649		1	0.117	East
Red-necked Phalarope					
Red Phalarope	13.156	1	2	0.129	Coastal and west
Lapland Longspur	22.335	1	2	0.201	Inland and east

DISCUSSION

Use of Coastal Habitats

Nesting

Arctic coastal tundra has rarely been described as having special attributes for nesting birds. Some arctic birds have narrow coastal distributions, especially those birds associated with islands or the ocean such as Common Eider (Schamal 1974, Wiggins and Johnson 1992) and Black Guillemot (Divoky et al. 1974), but these species are not expected to occur with any regularity in mainland tundra. Other species, such as Spectacled Eider and Red Phalarope, are often characterized as having coastal distributions. This is true only when *coast* is defined on a broad scale such as the Arctic Coastal Plain. In the central Beaufort region, the Arctic Coastal Plain is tens of kilometers wide, encompassing much of the Prudhoe Bay area. During the breeding season, most activity of birds is centered in tundra, not littoral areas (Connors et al. 1979). One of the few reported examples of selective use of coastal wetlands during the nesting season is of King Eiders (Bergman et al. 1977).

Our sampling indicates that coastal habitats are somewhat more distinctive than might have been expected based on the background summarized above. Baird's Sandpiper and Ruddy Turnstone were prominent members of the coastal nesting community, but these species occur only incidentally elsewhere in the Prudhoe Bay area and generally in disturbed habitats. That these two species were found in all three types of coastal plots suggests that proximity to the coast rather than sampling of some particular habitat type (e.g., dry plots) was important to them. Even including these specialists, the plots sampling the most strictly coastal habitats (saline and dry plots) supported relatively low nest densities. Nonsaline coastal plots sampled a habitat type that appears to have characteristics preferred by some of the common Prudhoe Bay area breeding birds, especially Semipalmated Sandpiper, Lapland Longspur, and Red-necked Phalarope. Nest density of Semipalmated Sandpiper in this plot type was almost twice as high as any other plot type sampled in 1991 (36 nests/km^2 on nonsaline plots vs. 19 nests/km^2 on saline plots). Overall, none of the coastal habitat associations sampled supported a nesting community as diverse as the PMRA, which is just slightly farther inland.

The stepwise regression analyses indicated that plot location was an important determinant of densities for several species. Although distance from the coast was involved in the regression model for more species (five) than was the east/west location (four), on the basis of the r^2 values the east-west gradient was stronger when it occurred. The coastal gradients indicated that Stilt Sandpiper, Red-necked Phalarope, and Lapland Longspur nest densities increased with increasing distance inland, whereas Dunlin and Red Phalarope nest densities were highest near the coast. The strongest coastal gradients were for Stilt Sandpiper, Red Phalarope, and Lapland Longspur. Based on the regression lines (Fig. 8), the expected nest densities (nests/km^2) of these species at the coast compared to 20

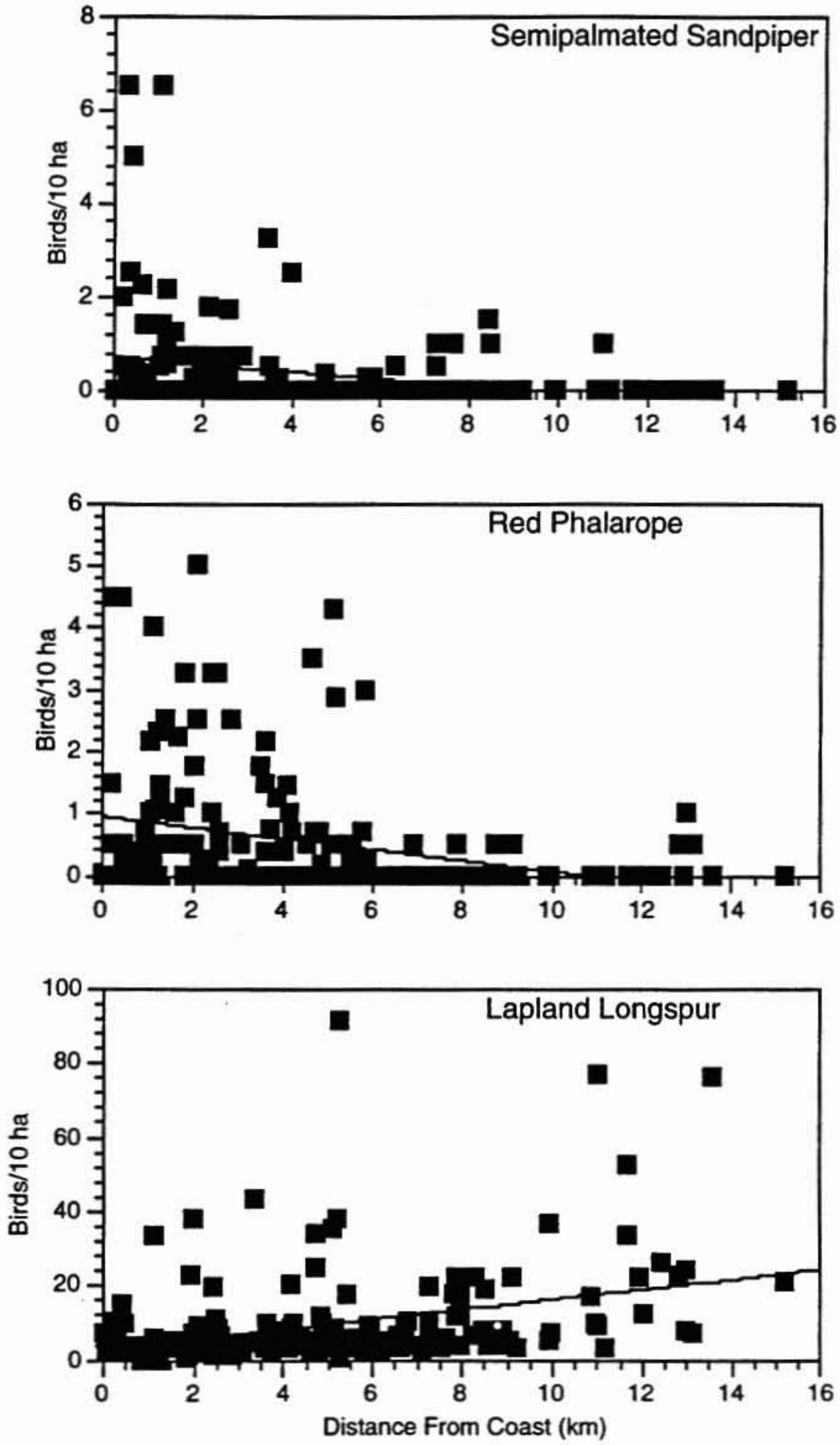

Figure 10. Trends in post-breeding-season densities in relation to distance from coast of Semipalmated Sandpiper, Red Phalarope, and Lapland Longspur.

km inland would be as follows: Stilt Sandpiper, 0.0 vs. 3.2; Red Phalarope, 6.6 vs. 1.6; and Lapland Longspur, 16.5 vs. 24.4. Inspection of the density profiles for these species (Fig. 8) reveals that the coastal zone is quite broad, if it can be defined at all. Stilt Sandpiper has not been found nesting at a measurable density within 1 km of the coast, and densities have been quite low within 10 km of the coast. Farther inland, Stilt Sandpiper nest densities are variable but can be considerably higher. Red Phalarope densities vary more at all distances from the coast than do Stilt Sandpiper densities; however, there is a tendency for higher Red Phalarope densities within 10 km of the coast than farther away. The trend in Lapland Longspur nest densities was the most gradual of the three and exhibited no indication of zonation along the range sampled.

The nest data provide weak evidence of coastal zonation. No species had a high degree of reliance on specific coastal habitats, but Baird's Sandpiper and Ruddy Turnstone appear to have an affinity for strictly coastal locations, generally within 1 to 2 km of the coast. On a broader scale there was some evidence of a discontinuity approximately 10 km from the coast (roughly at the Spine Road). Stilt Sandpiper nest density increased markedly inland of this demarcation, whereas Red Phalarope nest densities were highest shoreward of this distance. This corresponds to the zone of rapid temperature flux reported by Walker et al. (1980).

Seasonal Use by Birds

The attachment of birds to their nest sites would lead to the expectation that densities of birds would remain stable during the nesting season. The census data, however, indicate a remarkable amount of flux in bird populations during this time period. Shorebirds provide good examples of the dynamic nature of abundance fluctuations. The basic pattern in shorebird abundance trends on the North Slope has three phases: 1) arrival and nesting, 2) a July pulse corresponding to the outbound migration of adults, and 3) an August pulse corresponding to the outbound migration of juveniles (Connors et al. 1979) (see, for example, Lesser Golden-Plover or Pectoral Sandpiper in Fig. 4). This basic pattern may be modified depending on the species. For example, species with uniparental incubation such as Pectoral Sandpiper and phalaropes may have two pulses of adult migrants, the first in June overlapping with incubation and the second following hatch.

Our analyses of bird densities divide the summer into three periods—breeding, brood-rearing, and post-breeding—based on major components of the nesting cycle. Migrants may be recorded on censuses during all these periods, especially during the brood-rearing period.

Breeding Season. During the breeding season the coastal habitats were not expected to be of particular significance to birds. Saline and other coastal tundras have not been described as being of particular importance to nesting birds, with the possible exception of King Eider (Bergman et al. 1977). Some species, such as Semipalmated Sandpipers, nesting in nearby areas may make use of coastal habitats (Connors et al. 1979), but no major concentrations have been reported.

The results of this study generally support the prevailing idea that coastal habitats are not especially important during the breeding season. Many significant differences were found among plot types, and all of these differences were largely because of low densities on dry plots. As was found based on the nest data, the PMRA supported the most diverse bird assemblage during the breeding season, with six of the ten study species having their highest densities in this region slightly removed from the coast. The nonsaline coastal tundra, however, had considerably higher densities of Semipalmated Sandpiper and Lapland Longspur than any other plot type.

Red and Red-necked phalaropes had the greatest affinity of any of the study species to saline plots. Densities of these species were higher on this plot type than any other, although the differences among plot types were not significant. The nest data did not indicate any particular attraction of phalaropes to saline tundra. Phalaropes have uniparental incubation, with the males performing all the incubation and early brood-rearing (Schamel and Tracy 1977). This frees the females to begin their outbound migration during late-June. Our data show a pulse in densities in late June (Fig. 4), with a disproportionate number of birds in saline tundra, at least in the case of Red-necked Phalarope. This suggests that saline tundra is being used primarily by staging or migrant phalaropes.

The analyses of broad-scale geographic patterns revealed that almost all the study species had significant density gradients in either coastal or east-west orientations. The east-west gradient affected marginally more species (seven) than the coastal gradient (six). The magnitude of geographic effect was especially high for Stilt Sandpiper (32% of the variability) and Dunlin (23% of the variability). The species exhibiting