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Correlations Between Seabirds and Oceanic Fronts Around the Pribilof Islands, Alaska

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Located on the extensive continental shelf of the Bering Sea, the Pribilof Islands, Alaska are the site of one of the largest breeding colonies of seabirds in the northern hemisphere. During summer these islands are surrounded by a front that separates vertically homogeneous waters from well stratified waters farther seaward. We studied the front with hydrographic data and the bird distributions with concurrent counts during summer 1977 and spring, summer and fall 1978. Murres (*Uria lomvia* and *U. aalge*) sitting on the water aggregated near the front during summer 1977 and probably during summer 1978. Other species, such as northern fulmars (*Fulmarus glacialis*) and auklets (*Aethia pusilla* and *A. cristatella*) were unaffected by the front. We hypothesize that the aggregation of the murres was related to an enhanced availability of their food near the front.

Introduction

Oceanic fronts have long been recognized by oceanographers, and there has been a belief that fronts affect the abundance of marine organisms. With the notable exception of upwelling fronts, however, evidence for these effects has been mostly qualitative or anecdotal. Recently quantitative investigations of biological effects near shelf and shelfbreak fronts have appeared (e.g. Savidge, 1976; Fournier *et al.*, 1977, 1979; Pingree *et al.*, 1978; Iverson *et al.*, 1979*b*; Simpson *et al.*, 1979; Ainley & Jacobs, 1981; Bowman *et al.*, 1981). Such studies show that oceanic fronts indeed have significant impact on the marine ecology of some regions.

Distributions of seabirds, which occupy an upper level in the trophic web, can supply one clue to the interaction between biological and physical processes. Seabird distributions have been hypothesized to be related to the oceanic-scale variations in the availability of food (Bourne, 1963; Ashmole, 1971) as well as to other variables (Gould, 1971). Pocklington

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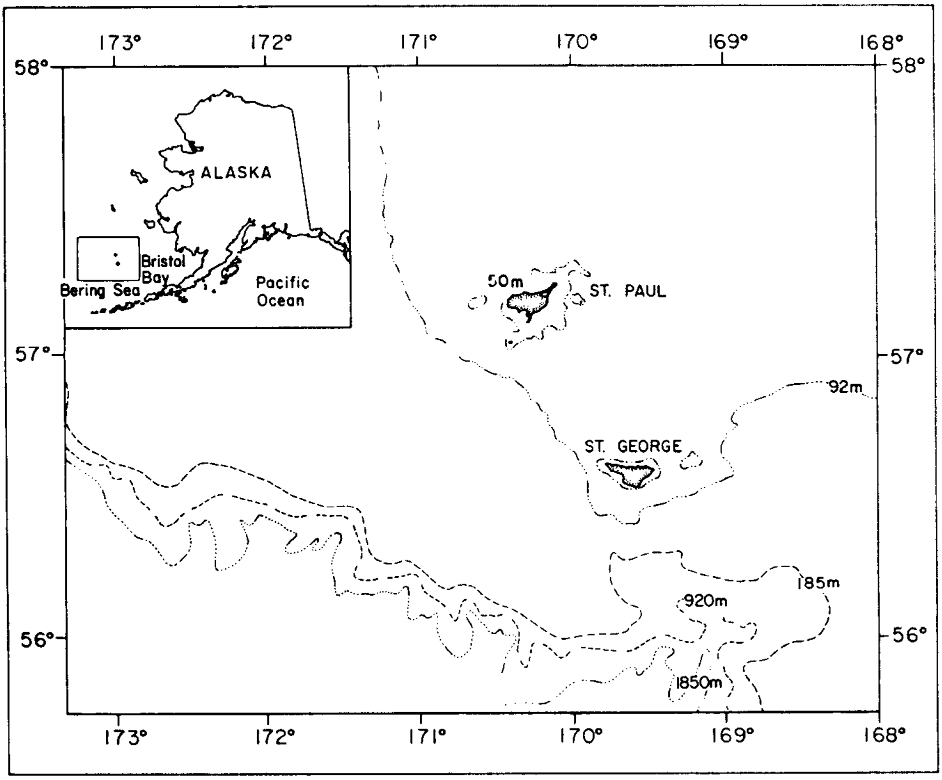

Figure 1. The Pribilof Islands, Alaska. St. Paul is surrounded by a large region with depths less than 50 m, while St. George is close to waters greater than 50 m depth.

(1979) demonstrated a relationship between water masses and bird communities in the Indian Ocean, and Hunt & Schneider (in preparation) have shown significant relationships between bird communities and water masses in the southeastern Bering Sea. Quantitative relationships between medium-scale (10–100 km or so) physical features and seabird concentrations have rarely been established, in part because this requires concurrent ornithological and oceanographic measurements.

During 1977 and 1978 we made coordinated hydrographic measurements and bird counts in the vicinity of the Pribilof Islands in the southeastern Bering Sea (Figure 1). These islands are relatively isolated: the nearest land is the Aleutian Islands about 300 km distant. The Pribilofs sit on the 500 km wide continental shelf about 30 to 100 km north of the shelfbreak.

The islands are breeding sites for herds of up to $1{\cdot}4 \times 10^6$ northern fur seals (*Callorhinus ursinus*; Baker *et al.*, 1970) and they have colonies numbering $2{\cdot}75 \times 10^6$ seabirds (Hickey & Craighead, 1977): northern fulmars, black- and red-legged kittiwakes (*Rissa trodactyla* and *R. brevirostris*), thick-billed and common murres, least and crested auklets, parakeet auklets (*Cyclorrhynchus psittacula*), horned puffins (*Fratercula corniculata*) and tufted puffins (*Lunda cirrhata*). Dark-bellied shearwaters (*Puffinus griseus* and *P. tenuirostris*) move into the Bering Sea from the southern hemisphere during summer. Although many of these species are seasonal residents, their food requirements must represent a large part of upper trophic web predation in the Bering shelf ecosystem.

Satellite infrared images (Plate 1) show that zones of relatively cold water surround each of the Pribilof Islands during summer. Those zones appear similar to the region of well

Plate 1. Satellite infrared image obtained on 1 August 1977. Light areas are cooler, and the patches surrounding the Pribilofs correspond to the well mixed water [cf. Figure 2(a)]. In the original, the surface waters are obviously cooler near St. Paul (Northern island) than they are near St. George. Note the complex detail in the patch boundaries. The 50-m front farther inshore shows clearly, and a concurrent visible image identified clouds.

mixed waters found inshore of the front which parallels the 50 m isobath on the south-eastern Bering shelf (Schumacher *et al.*, 1979), where a system of three fronts separates the shelf into three hydrographic domains (Coachman *et al.*, 1980; Kinder & Schumacher, 1981). This frontal system has been shown to have dramatic consequences for the trophic web over the shelf east of the Pribilofs (Iverson *et al.*, 1979*a*; Schneider & Hunt, 1982). As we show in this paper, the zones of cold water surrounding the islands are set off from surrounding waters by fronts similar to those described by Schumacher *et al.* (1979).

Our hypothesis is that if the physical processes associated with the fronts strongly affect trophic relationships, then a significant correlation should exist between the physical variables that define frontal locations and the distribution of seabirds. We first describe the fronts surrounding the islands, and then we show the small but significant correlation between the bird distributions and the fronts.

Methods

During August 1977 and April–May, August and September 1978 we made bird counts and hydrographic measurements during four cruises of about 5 days each. Bird counts were taken during daylight hours (unless prohibited by fog) and hydrographic measurements were made at night. We took a total of 1378 bird transects (649 in summer), did 122 hydrographic (CTD) profiles (58 in summer) and did 224 temperature (XBT) profiles (99 in summer).

Bird counts were made by the transect method (Burnham *et al.*, 1980) modified for use at sea. Counts were made while the ship was underway and all birds within 300 m of the ship were recorded during each 10-min count. At typical ship speeds, each counting period corresponded to about 1 km^2 of ocean surface. Species were identified to the lowest possible taxonomic level based on distinctive field marks. Ship-following individuals were noted to prevent duplicate counts. Sea surface salinity and temperature were measured during each 10-min transect.

During hours of darkness, when counting was impossible, we did hydrographic sections in the vicinity of the islands. We used a continuous conductivity–temperature–depth profiling instrument (CTD) which was accurate to better than 0·02 °C and 0·01‰ in temperature and salinity when averaged to 1 m values. During summer and fall of 1978 the CTD profiles were supplemented by expendable bathythermographic (XBT) drops, which yielded tempetatures within 0·2 °C.

The limited hydrographic measurements were used to define the frontal structure and location. We regressed bird density against five environmental variables; distance to shelf-break, distance to land, water depth, sea surface salinity, or sea surface temperature. Statistical analysis was done using the Statistical Package for the Social Sciences (SPSS: Nie *et al.*, 1975).

Fronts around the Pribilofs

During the three seasons covered by our surveys, spring, summer and fall, we found that the water columns were always well mixed near the islands and much less so farther from the islands. The transition between these well mixed and well stratified waters is abrupt (when viewed from a shelf-wide perspective) and it is therefore called a front (Schumacher *et al.*, 1979). This front is most strongly developed during summer and its surface manifestation is clearest then, so we emphasize summer data.

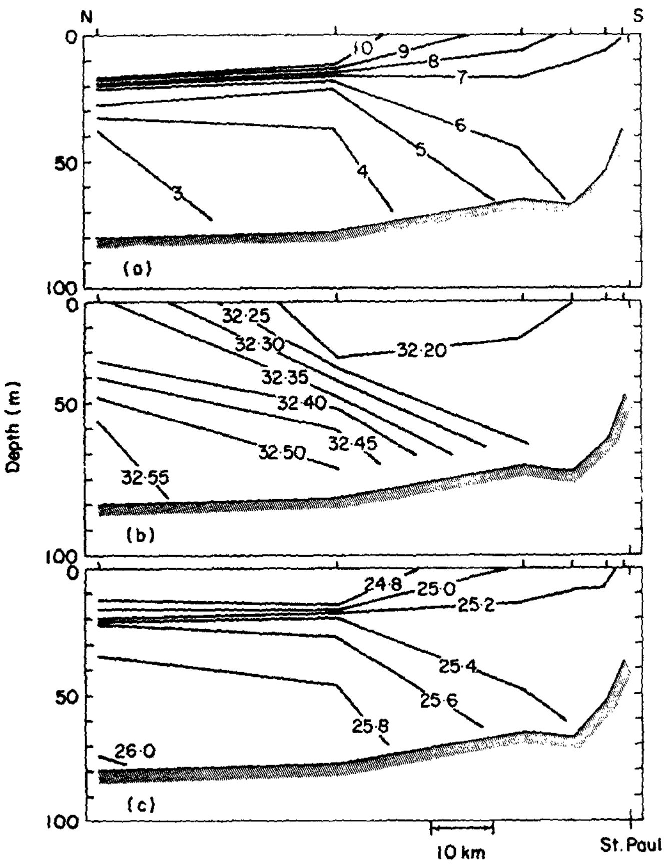

Figure 2. A hydrographic (CTD) cross-section taken north of St. Paul island on 5 August 1977. (a) Temperature (°C), (b) salinity (‰), (c) density (σ_t, kg m^{-3}). The strong two-layer stratification north of the island becomes nearly homogeneous in the shallow depths near the island.

A CTD section taken north from St Paul Island on 5 August 1977 illustrates the frontal structure (Figure 2). Away from the island the water column was strongly stratified in two layers: a 20-m thick upper layer, a 50-m thick lower layer and a 10 m thick pycnocline. Differences in temperature, salinity and density (σ_t) between the layers were 8·1 °C, 0·2‰, and 1·2 kg m^{-3}. At the station closest to shore, however, the 37-m deep water column was nearly homogeneous. Maximum vertical temperature, salinity and density differences were 0·08 °C, 0·01‰ and 0·01 kg m^{-3}.

This section is typical for summer: isotherms, isohalines and isopycnals are congruent. There is strong (often two-layer) stratification present away from the islands in deeper water, and weaker stratification present close to the islands in shallower water. When temperatures or density differences were plotted on a chart of the area, lines of equal stratification surrounded each island. While 40 stations (August 1977) were inadequate to clearly delineate the entire pattern, the satellite infrared image taken on 1 August (Plate 1) confirmed the inferred temperature pattern. This image is an exceptionally cloud-free summer view of the Bering shelf, and it shows two large areas of cooler (lighter gray) water surrounding each island. In the original image the patch surrounding St. Paul is lighter (i.e. colder) than that around St. George. We interpret these patches as the upward mixing of the colder lower layer water (Figure 2). The waters near St. George are less well mixed than those around St. Paul, probably because of the generally deeper water close to St. George (Figure 1): the capacity of the mixing process is inversely proportional to water depth (Schumacher *et al.*, 1979; Simpson & Pingree, 1978).

The spring (27 April–3 May) and autumn (23–27 September) 1978 data showed changes from the summer (August 1977 and 1978) structure. In both spring and autumn the pattern of stratification away from the islands and well mixed waters close to the islands obtained. In spring, however, stratification was due to relatively warm and salty water from the slope region intruding near the bottom, similar to the situation described by Coachman & Charnell (1979). In autumn, the surface signature of the front had disappeared and the upper 20–30 m was horizontally uniform, probably as a result of the onset of seasonal cooling. These spring and autumn structures fit into an annual pattern (Kinder & Schumacher, 1981), but we are only able to show a relationship between bird numbers and hydrographic data for summer.

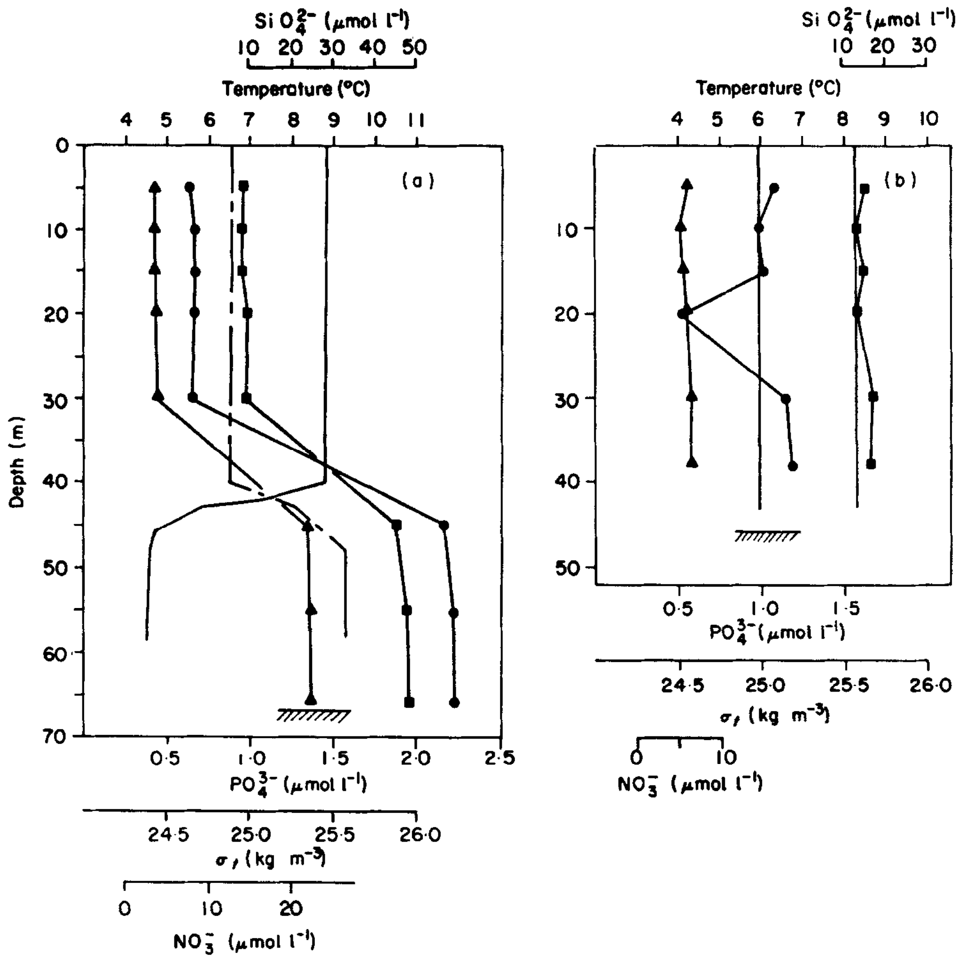

Figure 3. Vertical profiles of temperature (——), density (– – –), PO_4^{3-} (●—●), NO_3^- (▲—▲) and SiO_4^{2-} (■——■) at (a) Station 212 (57°48·4′N, 170°26·4′W) and (b) Station 194 (57°14·5′N, 170°25·2′W) during September 1978.

During the September 1978 cruise we also obtained nutrient samples at 13 stations. Station 212 was located about 65 km north of St. Paul in well stratified water while Station 194 was taken within 10 km of the north-western tip of the island in well mixed water (Figure 3). At Station 212 phosphate, silicate and nitrate were higher in the lower layer than in the upper layer by factors of 3 to 6, but upper layer nutrients remained high (0·6 µmol PO_4^{3-} l^{-1}, 8·8 µmol SiO_4^{2-} l^{-1} and 3·4 µmol NO_3^- l^{-1}). Nutrients were almost vertically uniform at Station 194; and the concentrations were intermediate between the upper and lower layer values at Station 212.

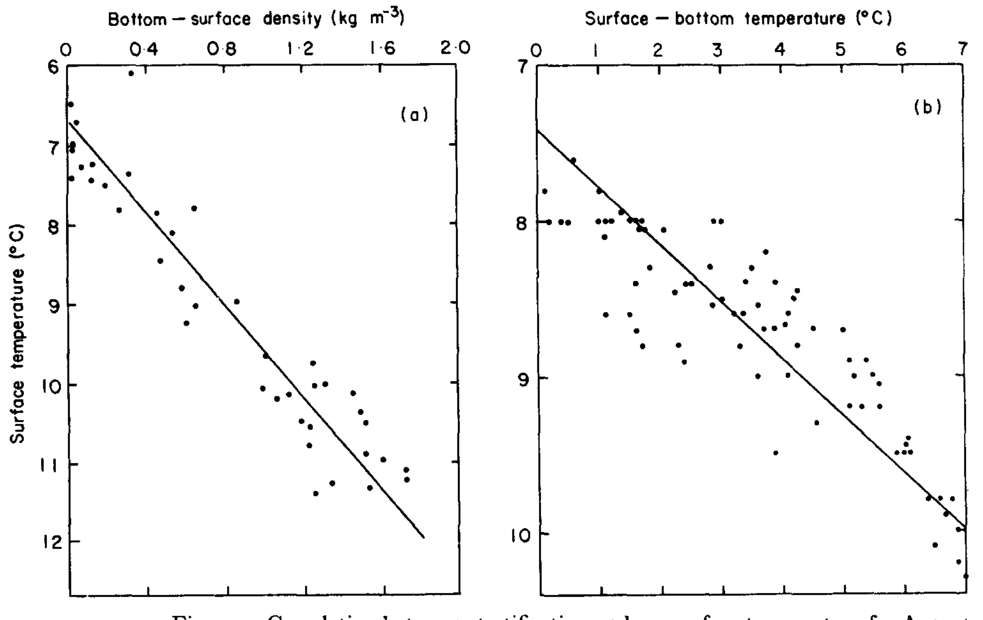

Figure 4. Correlation between stratification and sea surface temperature for August data. (a) 1977, (b) 1978. Temperature differences were used instead of density differences for 1978 data because of the abundance of XBT data. In (a) $\Delta\sigma_t = 0{\cdot}34T_s - 2{\cdot}25$; $n = 40$, $r = 0{\cdot}95$. In (b) $\Delta T = 2{\cdot}7T_s - 20{\cdot}4$; $n = 84$, $r = 0{\cdot}90$.

Correlation between bird counts and sea surface temperature

Sea surface temperature, which was measured during each bird count, was a valid measure of stratification during the two August cruises. In 1977 the regression of vertical density difference accounted for 90% of the surface temperature variance [Figure 4(a)]. During 1978, when temperature (XBT) data were much more abundant than density (CTD) data, vertical temperature difference accounted for 81% of the surface temperature variance [Figure 4(b)]. Thus, sea surface temperature was a useful variable for investigating the relationship between summertime stratification and bird counts. Data from the fall and spring cruise were excluded because of poor correlation between surface temperature and stratification.

Bird density is inversely related to distance from the breeding colonies due simply to geometric spreading as birds commute to and from the islands. Sea surface temperature (the explanatory variable) was also inversely related to distance from the island, because of the colder surface temperatures near the island. We controlled for the possible spurious correlation due to geometric spreading by introducing distance as a covariate in a one-way

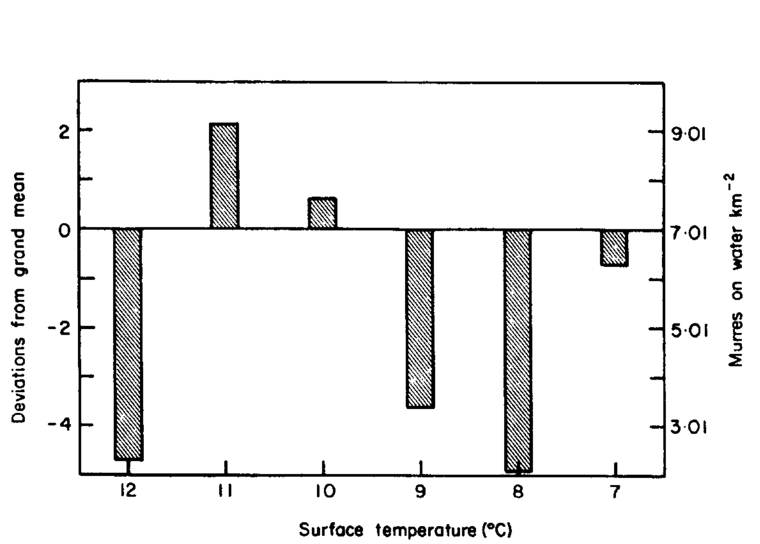

Figure 5. Analysis of variance for murres, August 1977. Deviations from the grand mean with distance as a covariate shows higher murre concentrations (on the water) near the seaward side of the front (Figure 6). The midpoints of 1·0° C wide temperature bins are plotted. ($N = 214$ counts in water depths <150 m.)

analysis of variance in bird numbers due to sea surface temperature. This is equivalent to regressing bird numbers against distance, then analysing the residuals from regression with respect to sea temperature. Results of this analysis are expressed as deviations from the grand mean, because of the adjustment for distance in the analysis. To be valid, this procedure requires that the effects of sea surface temperature and distance from the island be additive (independent) in their effects on bird numbers. For the August 1977 data three bird groups showed non-significant interaction effects in a two-way analysis of variance in bird numbers: murres ($P = 0·67$), auklets ($P = 0·37$) and fulmars ($P = 0·62$). Because the effect of geometric spreading was additive, it could be controlled statistically in subsequent analysis of these groups.

Murres on the water showed significantly higher density at the outer part of the front (10–11 °C, compare Figures 2 and 5). For all murres, including flying birds, density drops rapidly with distance from land, and the relation between water temperature and bird density is not significant ($P = 0·66$). A plot of all murres encountered along a single track parallel to the hydrographic section in Figure 2 showed the same result: decreasing numbers out to the front with a peak at 50–60 km, corresponding to the location of the front (compare Figures 2 and 6). Taken together, the statistical and graphical analyses indicate that murres fly outward from the colonies, decreasing their density by geometrical spreading, then aggregate on the water near the front.

Analyses of bird density relative to surface temperature, with distance controlled, were also made for auklets and northern fulmars. Auklets were confined to the immediate vicinity of the breeding colony and showed no significant relation between density and the water temperatures ($P = 0·10$). Fulmars, which forage at great distances from the breeding colonies, showed no significant relation between density and water temperature ($P = 0·15$). Of the three bird groups that showed independence between distance and temperature, only murres on the water had a significant association with surface temperature ($P = 0·014$).

The 1977 August results were checked by performing the same analysis on the August 1978 data. Again, there was a peak in density of murres on the water near the outer edge of the front (Figure 7). The probability of obtaining this result ($P = 0·03$) is the product of

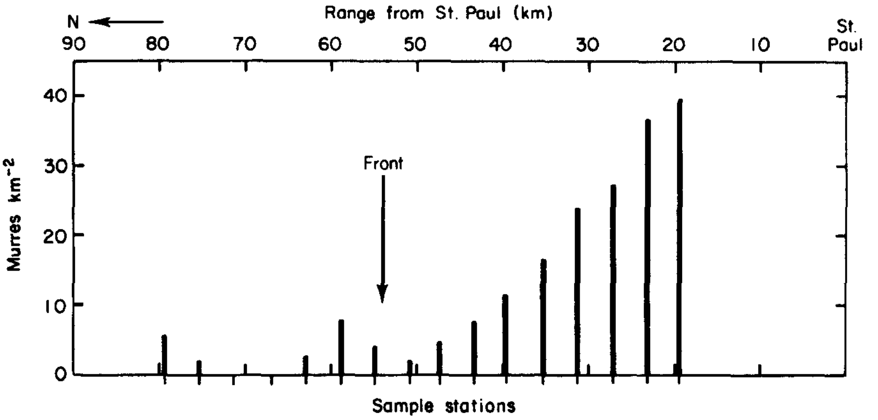

Figure 6. Murre density *vs.* distance, 5 August 1977. These data are from a section paralleling the hydrographic section in Figure 2. The major features are decreasing concentration with distance and a small relative increase near the front.

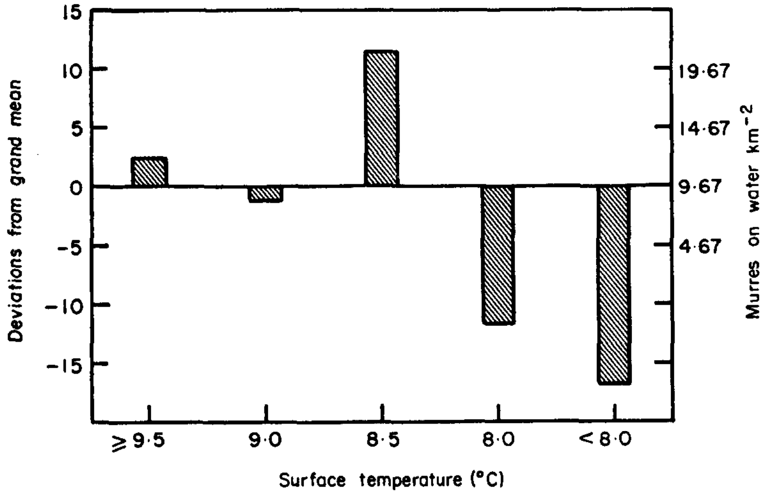

Figure 7. Analysis of variance for murres on the water, August 1978 (cf. Figure 5). The lower limits of 0·5 °C wide temperature bins are plotted. ($N = 232$ counts in water depth <200 m.)

the probability of obtaining a mean as extreme as that we observed ($P = 0{\cdot}17$) and the probability of having the largest mean coincide with the front (one chance in five, since five temperature classes were used).

We also compared the effects of several environmental variables on bird counts for all four cruises (Table 1). Multiple linear regression of bird density *vs.* distance to land, distance to the shelfbreak, water depth, sea surface temperature and sea surface salinity were used. This analysis was used because it is well understood and straightforward, even though the relationship of bird density on surface temperature, for example, was not linear. Significant results were obtained for each cruise, with a median of 8% explained variance. There is a trend for higher correlation in the August cruises than in the spring and fall cruises, especially among murres and northern fulmars. As anticipated, different species responded differently to the variables (e.g. murres, auklets and fulmars in August 1977 described above), so that

TABLE 1. Percentage variance explained by multiple regression of bird density on environmental variables[a]

Cruise	Murres	Northern fulmars	Black-legged kittiwakes	Red-legged kittiwakes	Auklets	*Puffinus* shearwaters	All birds on water
August 1977	27**	35**	14*	12*	20*	8	7
April–May 1978	6**	4*	7**	17**	6**	5*	7**
August 1978	15**	20**	14**	16**	5*	8**	8**
September 1978	5*	6*	15**	14**	7*	<1	6*

[a]The environmental variables were: distance to land, distance to the shelfbreak, water depth, sea surface temperature and surface salinity; * signifies $P<0{\cdot}05$; ** signifies $P<0{\cdot}001$.

grouping all birds together reduced explained variance. There were statistically significant correlations between bird densities and environmental variables, including frontal variables, but the explained variance was low. Obviously the front, while significant for murres, is only one factor in explaining seabird distributions around the Pribilofs.

Discussion

We have demonstrated the existence of shelf fronts around the Pribilof Islands and higher densities of sitting (probably feeding) murres near these fronts during summer. Correlations between the fronts and other populous species of seabirds were not significant. An important question is: what causes this preference for the front?

The link between the birds and the water column is probably trophic because the murres were on the water and probably feeding. Murres feed on juvenile walleye pollock (*Theragra chalcogramma*) in size ranges of 2–15 cm (Hunt *et al.*, 1981). These pollock in turn typically feed on large-bodied zooplankton (Clarke, 1978). Murres can dive to greater than 40 m depth (Tuck, 1960), that is, down to typical pycnocline depths in the stratified waters. The relationship between the front and the murres probably includes not only pollock and their prey, but the next lower level(s) in the trophic web as well. An important clue may be that a diving bird, such as the murres, concentrated at the front while a non-diving bird, such as the fulmar, did not.

Murres might preferentially feed near the front because of higher productivity or because of greater food availability. Arguments for increased productivity near fronts (e.g. Pingree *et al.*, 1975) often have been based on nutrient depletion in the upper layer, but nutrient concentrations in our study area apparently remain high even in the upper layer of the stratified water (Figure 3). Availability of food might be enhanced by horizontal convergences in the cross-frontal circulation patterns such as appear in the model of James (1978). Such convergences, either surface or especially subsurface, would concentrate organisms that attempt to actively or passively maintain their depth. Alternately, the pycnocline itself may provide the stability necessary for increased production (e.g. Pingree *et al.*, 1978) or for the accumulation of food particles.

In order to understand the concentration of seabirds near the front, a knowledge of the activities of the phytoplankton, zooplankton and pollock near the front is required. As a first step we suggest an integrated sampling program that includes simultaneous sampling of the physical environment (including frontal circulation) and the various levels of the trophic web. This would be extension of work now being done over the shelf east of the Pribilofs (Iverson *et al.*, 1979*a*).

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Note added in proof

On 5 August 1982 D. Schneider found a large concentration of murres feeding on euphausiids (not pollock) near the front northeast of St. George Island. A maximum in surface chlorophyll was present on the seaward side of the front.

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