

Foraging by murre (*Uria* spp.) at tidal fronts surrounding the Pribilof Islands, Alaska, USA

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ABSTRACT: We investigated the foraging distribution of 2 species of murre (*Uria lomvia* and *U. aalge*) in relation to Acoustically Determined Biomass (ADB) and hydrographic structure surrounding the Pribilof Islands, Bering Sea, Alaska, USA. The distribution and abundance of both murre species were similar; therefore, we combined data for thick-billed and common murre in the analysis. We found that murre densities were higher in frontal regions than in non-frontal regions. Maximum ADB was also found to be elevated in the frontal zone. Within frontal regions, high densities of murre were associated with regions containing relatively high levels of ADB. In contrast, we did not find significant correlations between murre density and ADB in the study area as a whole. We postulate that murre restrict their foraging to the frontal region because prey can be located more predictably within this zone than in other areas in the vicinity of the Pribilof Islands.

KEY WORDS: Seabird distribution · Tidal fronts · *Uria lomvia* · *Uria aalge* · Murre · Bering Sea

INTRODUCTION

Shelf-sea fronts have been identified as regions of persistent high densities of phytoplankton, zooplankton and vertebrate predators (Holligan 1981, Hunt 1990, Franks 1992a, b). Physical processes associated with fronts enhance *in situ* production of phytoplankton and mechanically aggregate zooplankton, which may result in increased prey availability to predators, including seabirds. Spatially and temporally predictable feeding sites, such as those found at fronts, may be important to breeding seabirds that depend on consistent availability of prey near colonies to raise young successfully. In this paper, we examine the foraging distribution of thick-billed and common murre (*Uria lomvia* and *U. aalge*) in relationship to the tidal fronts surrounding the Pribilof Islands. We hypothesize that murre forage preferentially in the frontal region in response to enhanced abundance of prey there. To ensure foraging success, marine birds do not randomly sample the environment for prey, but instead they

focus their search efforts in areas where prey can be located predictably, and under-sample other areas, even though prey may be present.

Hydrographic fronts are defined as regions where steep horizontal gradients in temperature, salinity, density or velocity occur (Fedorov 1986). Shelf-sea tidal fronts are comprised of bathymetrically generated turbulence gradients, and occupy nearly constant locations (Simpson 1981). Flows associated with fronts can maintain the physical property gradients at the frontal interface, and can also increase the local biomass of phytoplankton and zooplankton by enhancing either the production or the accumulation of organisms in the frontal region (Pingree et al. 1974, Le Fevre 1986, Franks 1992a)

Many studies have shown that marine predators are attracted to spatially predictable aggregations of prey found in frontal regions. Relatively high densities of fish (Fiedler & Bernard 1987, Herron et al. 1989, Podesta et al. 1993), marine birds (Schneider 1982, Kinder et al. 1983, Haney & McGillivray 1985, Schneider et al. 1987, 1990, Brown & Gaskin 1988, Harrison et al. 1990, Hunt & Harrison 1990), and marine mammals (Brown & Winn 1989, McConnell et

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al. 1992) have been observed at fronts. Fronts with predictable aggregations of prey may be of particular importance for predators with elevated metabolic demands, such as those raising young (e.g. Kinder et al. 1983, Harrison et al. 1990, Hunt & Harrison 1990) or those preparing for migration (e.g. Brown & Gaskin 1988).

The Pribilof Island frontal system, a typical shelf-sea tidal front, was first described by Kinder et al. (1983). The front is the boundary between well-mixed near-shore waters and stratified offshore waters, and is located approximately at the 70 m isobath around each island (Fig. 1). Kinder et al. (1983) and Schneider et al. (1990) found that murre aggregated near the front in summer. The present study differs from previous studies in that we also examined the relationship between murre and Acoustically Determined Biomass in the frontal region. Our study of murre foraging extends the investigation of Coyle & Cooney (1993) which described elevated biomass in the frontal region.

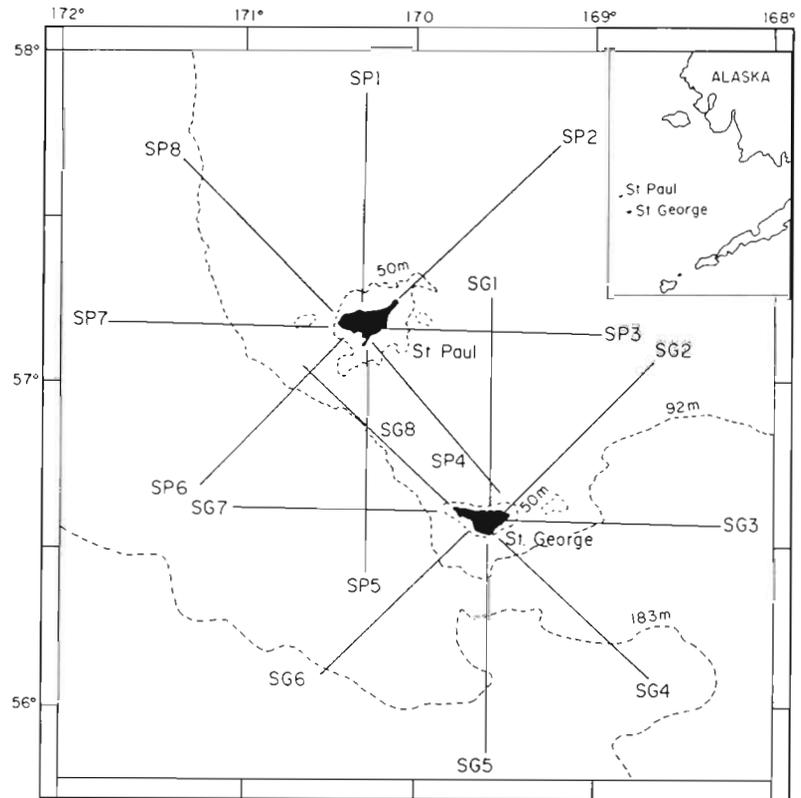


Fig. 1 Study area around the Pribilof Islands, Alaska, USA, and transects conducted in 1987 and 1988

METHODS

We studied the foraging distribution of thick-billed and common murre in relation to hydrographic features and ADB around the Pribilof Islands, Alaska, USA, during 26 July to 17 August 1987 and 28 July to 21 August 1988. Marine bird, hydroacoustic, and hydrographic data were collected in the vicinity of the Pribilof Islands during daylight hours along 74.1 km long transects radiating out from each island (Fig. 1). Each transect was completed twice each year, once to collect continuous bird and hydroacoustic data and once to collect bird data interrupted by CTD (Conductivity Temperature Density) stations.

Seabird censuses. To determine the foraging distribution of murre, continuous counts were made from the bridge of the RV 'Alpha Helix' while underway at speeds of 14.8 km h^{-1} during acoustic surveys and 18.5 km h^{-1} between CTD stations. All birds within an arc from 300 m ahead of the ship to 90° off the side with the best visibility were counted and data were entered in a hand-held microcomputer. Birds were recorded as flying, on the water or feeding. Murre found on the water were assumed to be foraging or to have been foraging recently, thus the

2 categories 'on water' and 'feeding' were combined into a 'feeding' category for analyses. We excluded flying birds from all analyses. We calculated average densities of murre for every 9.3 km along a given transect to correspond to the interval between CTD stations. The distributions and abundances of both thick-billed murre and common murre were similar. Therefore, we combined data from both species along with unidentified murre in the analyses. For every transect, average murre densities for each of the eight 9.3 km intervals were assigned to frontal or non-frontal categories (see below for definition of frontal regions).

During the breeding season, bird density is inversely related to distance from the colony due to geometric spreading as birds travel to and from the islands (Kinder et al. 1983). Birds counted on a 300 m strip of a radial transect represent only a portion of all the birds present in that sector of the ocean. To remove the effect of declining bird densities due to geometric spreading, we calculated an expected density for each transect interval. Our model assumed murre spread out evenly from the island and that an equal number of murre land in each 9.3 km distance interval between the island and the end of the transect. Expected murre

densities were estimated for each distance interval along a transect in the following manner. First we calculated the absolute number of birds in an entire sector by multiplying the observed density (birds km⁻²) in each 9.3 km distance interval along a transect by the area, where the area is equal to

$$1/8 \pi [R_{j+1}^2 - R_j^2]$$

where R is the distance from the island and j identifies the distance interval. The total number of birds present in a sector was divided by the number of intervals surveyed per transect to yield the expected number of birds per sector interval. We divided the expected numbers of murres by the area of a given portion of a sector to convert expected bird numbers to expected bird densities. The result is an expected density distribution for each transect that declines geometrically with increasing distance from the island.

In this model, expected murre density declined as a function of

$$1/8 \pi [R_{j+1}^2 - R_j^2]$$

This is a suitable model to use in this system as we found that the observed densities generally declined with increasing distance along each transect. We examined an alternative model in which expected densities declined as a function of

$$1/8 \pi [R_{j+1}^3 - R_j^3]$$

This model assumes murres prefer to forage closer to the island and that numbers drop off as a function of distance from the island. We did not use this model because the resulting expected density distributions vastly over-emphasized the use of near-shore waters by murres compared to what we observed at sea. The correct model for murre distribution around the colonies must fall between the 2 models above, but the one we chose to use is more conservative with respect to detecting the use of an offshore front.

The expected density value calculated for a given 9.3 km transect interval was subtracted from the density of murres observed in that same interval. We used this deviation from the expected density as the response variable in statistical analyses. In the remainder of the paper, we refer to the deviation as simply 'murre density anomaly' unless stated otherwise. Transects between the islands (SP 3, 4, 5 and SG 1, 7, 8; see Fig. 1) were excluded from the analyses to avoid miscalculations of expected densities in areas where murres from both islands were likely to forage. Bird densities were checked for spatial auto-correlation between adjacent 9.3 km transect intervals before performance of statistical analyses.

Physical oceanographic data. Data on water column structure were obtained by lowering a CTD

probe to within 5 m of the bottom at stations located 9.3 km apart out to 37.1 km from the islands and at stations located 18.5 km apart between 37.1 and 74.1 km from the islands. The location of the front on each transect was determined by calculating the difference in temperature between adjacent stations at 10 m depth intervals summed throughout the water column (Schneider 1982). For each transect, the location of the front was determined to be between the 2 stations having the highest horizontal gradient in temperature. In our study, the 'frontal region' included 2 adjacent transect intervals (18.6 km); one with the strongest temperature gradient and the other on the seaward side where the pycnocline deviates from the horizontal (Franks 1992a). We included the seaward transect interval in the frontal region because elevated levels of biomass and chlorophyll were commonly observed in the stratified water on the seaward side of the Pribilof front (Schneider et al. 1990, Coyle & Cooney 1993). Theory suggests that the width scale of tidal fronts is usually greater than 5 km and that phytoplankton patches associated with fronts are 5 to 10 times greater than the cross-frontal width (Franks 1992a). Therefore, the width scale of the 'frontal region' in this study is a conservative measure.

Hydroacoustic data. Acoustic data were collected with a 200 kHz BiosonicsTM model 101 echosounder and a model 120-121 echo integrator. The transducer was mounted in a 1 m V-fin and towed beside the ship 5 m below the surface at 14.8 km h⁻¹. Echo returns were blanked to 5 m below the transducer and at 5 m above the bottom to reduce near-surface noise and bottom integration. Murres typically feed in water deeper than 10 m (Croll et al. 1992); therefore, blanking the biomass records from the upper 10 m should not significantly affect our results. The echo integrator resolved sound scattering intensity in thirty 5 m depth intervals from 10 to 160 m. A horizontal distance of approximately 0.37 km was integrated for each sample along the transects. Coyle & Cooney (1993) describe the methods used to calibrate the acoustic equipment for both the 1987 and 1988 cruises.

A target estimate of -60 dB was applied to all data to convert echo return voltages to estimates of biomass in g m⁻³. Using a target strength of -60 dB, the acoustic biomass estimates roughly approximated the biomass found in net samples. However, the target strengths of a diverse zooplankton community are variable and should not be expressed as a single value (Greene et al. 1989). Therefore, hydroacoustic data are considered to be relative measurements of biomass along transects. Mean Acoustically Determined Biomass (ADB) was calculated by averaging

the biomass estimates throughout the water column for each 9.3 km interval along a transect. Maximum biomass was the highest biomass value within each 9.3 km transect interval. Biomass was also categorized as either 'high', where the mean biomass value of the transect interval was greater than the overall transect mean, or 'low', where mean biomass value of the interval was less than transect mean. Patches of acoustic biomass were identified as aggregations of ADB greater than a biomass value of 1 g m^{-3} in a 9.3 km transect interval. We considered acoustic biomass patches measuring 1 g m^{-3} or more to be a significant aggregation of prey since 92.3% of the ADB 1 m averages were less than 1 g m^{-3} .

Stomach contents. Foraging thick-billed and common murres were collected at 2 locations ($56^{\circ} 38.4' \text{ N}$, $169^{\circ} 24.7' \text{ W}$ and $56^{\circ} 44.4' \text{ N}$, $169^{\circ} 34.5' \text{ W}$) using a 12-gauge shotgun from either the bow of the ship or from a skiff during the 1987 cruise. The proventriculus and ventriculus were removed, split and placed in 80% ethanol promptly after collection. Stomach contents were identified to the lowest taxonomic level possible. The number of fish otoliths and euphausiid eyes were divided by 2 to estimate the number of fish of a given taxon, and unidentifiable euphausiids respectively, in a sample. The percentage by number and percentage of occurrence were tabulated for each prey item. Percentage number and percentage volume are percent-

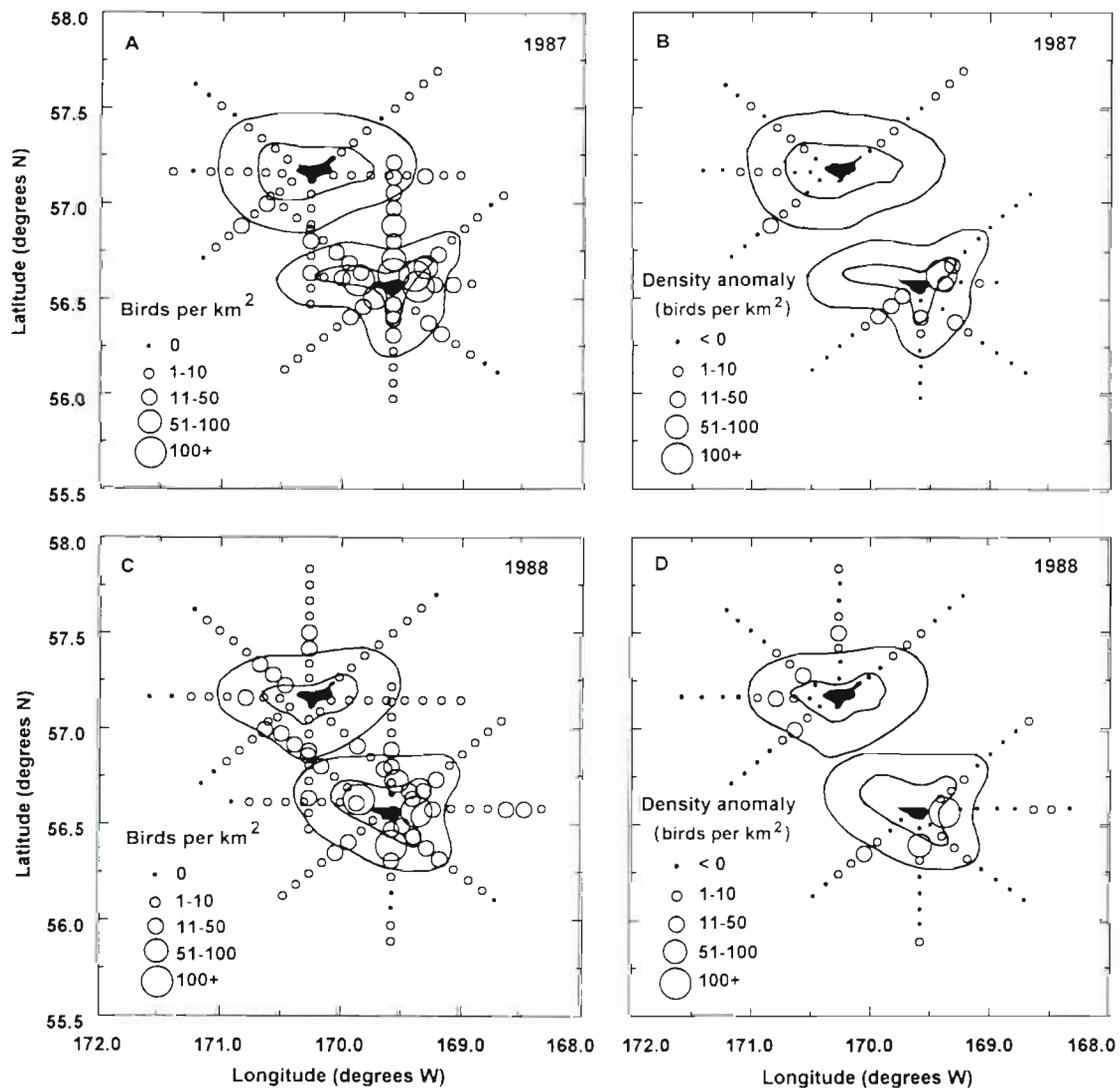


Fig. 2. Distribution of observed murre (*Una* spp.) density (A and C) and murre density anomalies (B and D) on acoustic transects in 1987 and 1988. Annuli indicate location of frontal regions surrounding St. Paul and St. George Islands, 26 July to 17 August 1987 (A and B) and 28 July to 21 August 1988 (C and D)

age compositions of prey species for all stomach samples combined. Percentage of occurrence is the proportion of all birds containing a particular prey item.

Statistical analyses. Assumptions of normality of residuals and homogeneity of variances were tested before conducting parametric statistics. If the data violated these assumptions following log-transformation, then randomization (Manly 1991) or non-parametric tests were performed to evaluate statistical significance. To perform randomization tests, a Turbo Pascal program was used to obtain 100 random permutations of average murre density anomalies or maximum acoustic biomass, and these were reassigned to frontal categories. Expected F -ratios were obtained by conducting ANOVA on each randomization of the data set. The null hypothesis was rejected if the observed F -ratio exceeded 95 out of 100 expected values. The lowest anomalous murre density value was greater than -20 birds km^{-2} , therefore, in order to log-transform negative values, we added 20 to each density to create positive values. Yates' correction for continuity was applied to all chi-square tests of independence. All statistical analyses were performed using Systat for Windows 5.03. Differences were considered significant at $\alpha = 0.05$.

RESULTS

Murre density relative to hydrography

The location of the front varied along transects from 1 to 37 km from the islands (Fig. 2). We found that murre densities along transects generally declined with increasing distance from the islands but that densities were typically higher within frontal zones (Fig. 2A, C). Plots of murre density anomalies reveal a pattern of elevated murre abundance in the vicinity of the frontal zone in both 1987 and 1988 (Fig. 2B, D).

Data on murre, ADB and hydrography from a representative transect are presented in Fig. 3. On this transect, the frontal region was located between 9.3 and 27.8 km from St. Paul Island. A strong temperature gradient ($\Delta 2.5^\circ\text{C}$) at the front separated the well-mixed near-shore water from stratified offshore water. High levels of relative ADB (8.2 g m^{-3}) and chlorophyll (9.0 mg m^{-3}) were found at the front and on the offshore side of the front above the thermocline (Fig. 3C, D). Observed murre density was greater than expected in the frontal region, and was associated with elevated ADB in the frontal zone (Fig. 3A, C). Murre were not observed in association with a dense patch of ADB

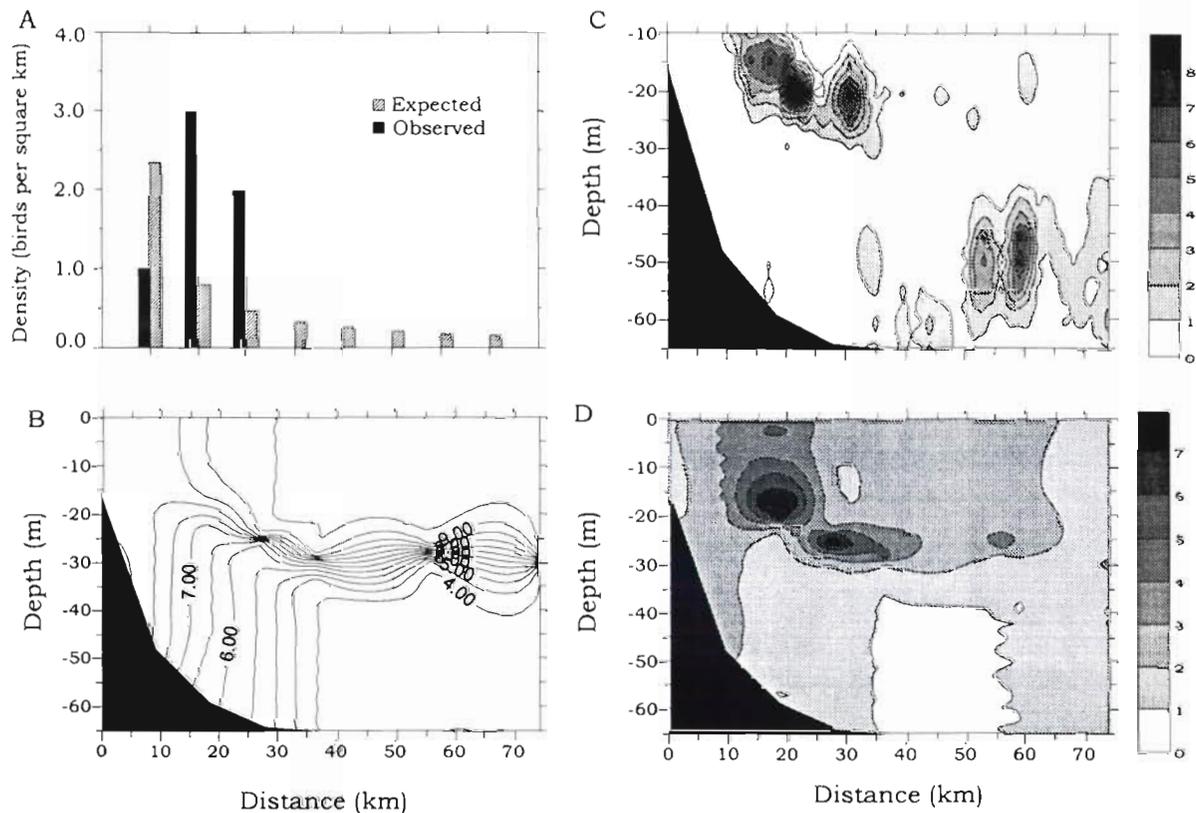


Fig. 3. Distribution of (A) observed and expected murre (*Uria* spp.) densities, (B) temperature ($^\circ\text{C}$), (C) Acoustically Determined Biomass (g m^{-3}), and (D) chlorophyll concentration (mg m^{-3}) along transect SP1 in 1987

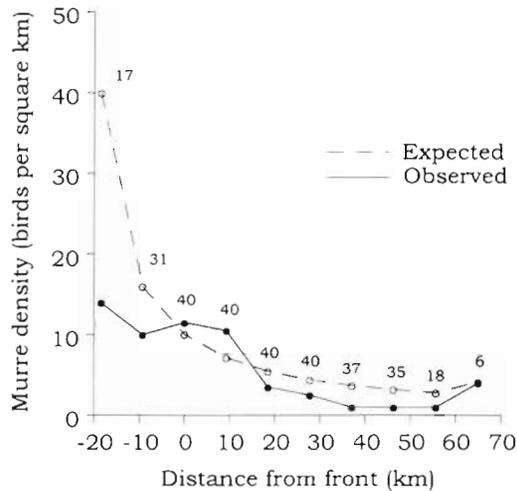


Fig. 4. Median observed and expected murre (*Uria* spp.) density (birds km⁻²) as a function of distance from the front. Sample sizes above each data point indicate number of transect intervals in each distance category. Negative distance values correspond to transect intervals located between the island and the front

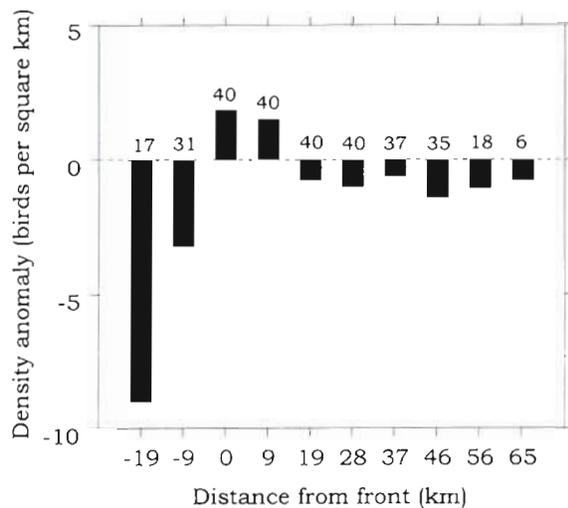


Fig. 5. Median deviation of observed from expected murre (*Uria* spp.) density (birds km⁻²) in relation to distance from the front. Sample sizes indicate number of transect intervals in each distance category

located 60 km along the transect at 50 m depth (Fig. 3A, C).

We sought to determine if this pattern of increased murre density at the front was consistent throughout the study area. To do so, median observed and expected densities of murres from all transect intervals were plotted as a function of distance from the front (Fig. 4); negative distances were located on the landward side of the front, zero was the location of the front

and positive distances were located on the seaward side of the front. The median difference between observed and expected murre density was plotted for each distance category (Fig. 5). One-sample sign tests of the deviation of observed from expected murre density indicated that the difference in murre density was significantly greater than zero in the frontal region (0 and +9.3 km from the front). Values in all other distance categories either were not significantly different, or were significantly less, than the expected value of zero. Results of a randomization test showed that anomalous murre densities were significantly higher in frontal zones than in non-frontal zones (observed 1-way analysis of variance $F_{1,302} = 2.087$, $p < 0.04$). The median observed murre density was 3.2 birds km⁻² (density anomaly of +0.48 birds km⁻²) in the frontal region and 0.88 birds km⁻² (density anomaly of -0.29 birds km⁻²) in non-frontal regions.

Acoustic biomass and murre density relative to frontal zone

Using a randomization test we found that peak ADB values were more commonly associated with frontal regions than non-frontal zones (observed 1-way analysis of variance $F_{1,143} = 5.34$, $p < 0.03$). The mean peak ADB was 6.4 g m⁻³ in the frontal region and 4.1 g m⁻³ in non-frontal regions. However, in the study area as a whole, we did not find murre density to be correlated with mean or maximum acoustic biomass ($r = 0.07$, $p = 0.38$, $df = 144$ and $r = 0.16$, $p = 0.06$, $df = 144$ respectively) at the scale of 9.3 km. These results suggest that even though acoustic biomass and murre density are relatively high in frontal regions, there are patches of biomass in the study area that are not attended by murres.

To test whether murres attended areas of elevated biomass within frontal zones more often than areas of elevated biomass away from fronts, we examined murre attendance in areas where biomass was greater than 1 g m⁻³ in frontal zones and non-frontal zones. Observations of vertical sections indicate that acoustic features were often characterized by ADB values greater than 1 g m⁻³, whereas background levels were typically less than 1 g m⁻³ (e.g. Fig. 3C). When we considered transect intervals in which patches of biomass greater than 1 g m⁻³ were present, murres were found to be associated with these patches within the frontal region more often than with patches away from the front (Table 1a; $\chi^2 = 15.5$, $df = 1$, $p < 0.001$).

We investigated whether murres passed over patches of acoustic biomass on the landward side of the front by performing the same test of independence as in Table 1a, but only for near-shore (between an island and the front) and front transect intervals

Table 1. A comparison of murre (*Uria* spp.) use of prey patches (Acoustically Determined Biomass > 1 g m⁻³) within (a) the frontal region surrounding the Pribilof Islands as compared to murre use of prey patches in non-frontal areas and (b) the frontal region surrounding the Pribilof Islands as compared to murre use of prey patches between the front and the islands

| Zone | Murre Density | |
|-----------------------|---------------------|---------------------|
| | Observed > Expected | Observed < Expected |
| (a) Front | 25 | 10 |
| Non-front | 17 | 44 |
| (b) Front | 20 | 5 |
| Near-shore, non-front | 7 | 11 |

(Table 1b). We found a significant association between murre density and frontal category ($\chi^2 = 5.91$, $df = 1$, $p < 0.025$). This result suggests that murre passed over near-shore patches of acoustic biomass and preferentially fed in frontal zones.

We conducted a 2-way ANOVA to test whether murre density anomalies were significantly higher in frontal regions than in non-frontal regions, and whether variation in murre density could be explained by ADB when defined as higher or lower than the mean value for the transect. A randomization test showed a significant interaction between the front and prey biomass (observed interaction $F_{1,141} = 6.312$, $p < 0.0001$) suggesting that high prey biomass within the frontal region affects murre density. Therefore, we examined the main effects separately for each category. A randomization test was used to evaluate statistical significance in a 1-way ANOVA. We tested for differences in the murre density anomaly between 4 categories: non-front/low acoustic biomass, non-front/high acoustic biomass, front/low acoustic biomass, and front/high acoustic biomass. We found that anomalous murre density was significantly different between groups (observed 1-way ANOVA $F_{3,141} = 2.521$, $p < 0.05$). A multi-comparison test between groups (Siegel & Castellan 1988) revealed that median murre density in frontal regions with high acoustic biomass was significantly different from median murre density in frontal regions with low acoustic biomass and in non-frontal regions having either high or low acoustic biomass (Fig. 6). All other comparisons between groups were non-significant.

Murre diets

Results from stomach contents of murre collected at 2 locations near St. George Island are presented in Table 2. Samples collected on 30 July 1987 were from

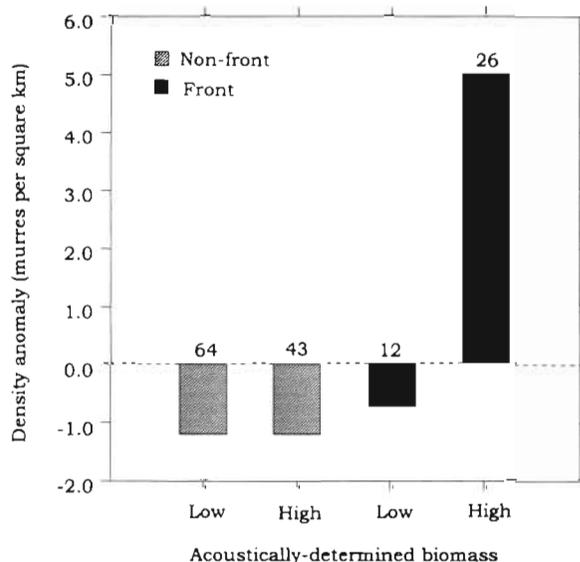


Fig. 6. Median deviation of observed from expected murre (*Uria* spp.) density (birds km⁻²) in 4 different frontal and acoustic biomass categories. Numbers indicate sample sizes

murre feeding on transect SG 2 on the 'mixed' or landward side of the front. Murre collected on 29 July 1987 were feeding at SG 1 on the 'stratified' or seaward side of the front. Thick-billed and common murre at both locations had been feeding on a diversity of prey species, consisting mostly of walleye pollock (*Theragra chalcogramma*) and euphausiids (*Thysanoessa* spp.). We did not observe any obvious differences in prey obtained at these 2 sites, with the exception of squid taken by murre feeding on the seaward side of the front.

DISCUSSION

Near the Pribilof Islands, peak acoustic biomass values were more commonly associated with frontal regions than non-frontal regions. These tidally generated fronts (Kinder et al. 1983) may be a zone of both enhanced production and physical accumulation of marine organisms. We interpret the presence of significant phytoplankton stocks in August as the result of the enhanced vertical influx of nutrients in the frontal zone (Coyle & Cooney 1993). Physical processes at the front may prolong the period of high primary production well into the summer, and mobile predators could be expected to be attracted to zones of relatively high productivity (Fogg et al. 1985). In addition, weakly swimming zooplankton are concentrated by convergences associated with tidal fronts (Pingree et al. 1974, Simpson 1981), and some of the accumulations of biomass in the tidal fronts at the Pribilofs may result from

Table 2. Stomach contents of murre (*Uria* spp.) collected near the Pribilof Islands in 1987 %Occ: percent occurrence; %Num: percent number; %Vol: percent volume (ml); ta: trace amount

| | Thick-billed murre | | | Common murre | | |
|--|--------------------|--------------|------|--------------|--------------|------|
| | %Occ | %Num | %Vol | %Occ | %Num | %Vol |
| 30 July 1987, 12:53 h, 56° 38.4' N 169° 24.7' W | | n = 4 | | | n = 2 | |
| <i>Theragra chalcogramma</i> | 100 | 95.9 | 61.0 | 100 | 96.0 | 87.5 |
| <i>Ammodytes hexapterus</i> | 25 | 0.3 | ta | 0 | 0 | 0 |
| <i>Mallotus villosus</i> | 25 | 0.3 | ta | 0 | 0 | 0 |
| <i>Thysanoessa raschii</i> | 0 | 0 | 0 | 50 | 4.0 | 12.5 |
| Unidentified crustaceans | 50 | 3.4 | 39.0 | 0 | 0 | 0 |
| 29 July 1987, 20:30 h, 56° 44.4' N 169° 34.5' W | | n = 5 | | | n = 1 | |
| <i>Theragra chalcogramma</i> | 20 | 27.3 | 0.07 | 56.3 | 30.0 | 30.0 |
| Gadidae | 20 | 11.1 | 0.07 | 0 | 0 | 0 |
| Unidentified fish | 20 | 11.1 | 0.7 | 0 | 0 | 0 |
| <i>Thysanoessa raschii</i> | 20 | ta | 14.8 | 37.5 | 30.0 | 30.0 |
| Euphausiidae | 60 | ta | 79.8 | 0 | 0 | 0 |
| Unidentified crustaceans | 40 | ta | 2.2 | 0 | 0 | 0 |
| Squid | 60 | 36.4 | 0.15 | 6.3 | 40.0 | 40.0 |
| Unidentified chondrichthyes | 20 | ta | 2.2 | 0 | 0 | 0 |

physical transport (Schneider et al. 1990) Whatever the source of these prey aggregations, they are important to predators that can benefit by the use of 'local knowledge' (Irons 1992) to find prey associated with relocatable oceanographic features.

The amount of ADB and murre varied among crossings of the tidal fronts. The strength of property gradients and associated currents at the front are likely to vary due to changes in tidal velocity and bottom topography (Simpson 1981). Seabird abundance has been related to gradient strength at hydrographic features elsewhere in the Bering Sea (Schneider et al. 1987, Hunt et al. 1990, Haney 1991) and in the Atlantic Ocean (Haney & McGillivray 1985). Thus, variability in the abundance of seabirds and their prey within the frontal zone surrounding the Pribilof Islands may be related to the variability in the strength of property or velocity gradients.

Coyle & Cooney (1993) found that the major component of the net tows from the mid-water acoustic features around the Pribilof Islands was gelatinous zooplankton, particularly large schyphozoans. Typically, Cnidaria are not themselves murre prey, although jellyfish do sometimes occur in murre diets (Harrison 1984). However, young stages of gadid fish are often associated with schyphozoans (Mansueti 1963, Van Hying & Cooney 1974). During this investigation, juvenile pollock were caught in net tows (Evans 1992) and were also present in murre stomach samples (Table 2). More recently, R. Brodeur (pers. comm.) observed juvenile pollock associated with gelatinous zooplankton near the Pribilofs. Hydroacoustic features in this study apparently are good indicators of the presence of murre prey in the frontal region.

Diets of murre reported in this study differ from those reported in other studies of murre foraging at oceanographic processes near the Pribilof Islands (Schneider et al. 1990, Coyle et al. 1992). In these studies, murre on the landward side of the front were feeding exclusively on euphausiids that were concentrated over a submarine ridge by tidal currents near St. George Island. Murre diets on both the landward and seaward sides of the front in our current study consisted of a mixture of euphausiids and pollock. Our diet results are similar to those for birds collected by Coyle et al. (1992) during slack water, when tidal currents were not strong enough to concentrate euphausiids.

Thick-billed and common murre foraged preferentially at the fronts surrounding the Pribilof Islands. Results from our study support the previously advanced hypothesis that these tidal fronts are important foraging areas for locally breeding seabirds (Kinder et al. 1983, Schneider et al. 1990). Patches within fronts are more likely to be attended by murre than patches found outside of the frontal area. We conclude that prey aggregations that can be found in a predictable location are more important to feeding murre and that prey abundance or distance from the colony are less important in determining bird distributions at sea. If marine birds focus their foraging on a relatively small portion of a study area, correlations between predatory birds and their prey may be stronger within the focal foraging area than within the larger region as a whole. If true, this relationship could explain why at a regional spatial scale marine birds are often weakly correlated with their prey (e.g. Heinemann et al. 1989).

Cairns & Schneider (1990) proposed that seabirds select foraging habitats influenced by coarse-scale (1 to 100 km) oceanographic features that concentrate prey at 'hot spots'. Seabirds can decrease foraging costs by focusing foraging efforts in spatially and temporally predictable feeding areas (Hunt et al. 1990, Schneider et al. 1990). Thus, the cost of commuting can be offset by higher foraging success within frontal areas (Obst et al. 1995). Murre are diving predators and their prey are presumably not visible from the sea-surface. It may be more profitable for murre to forage in areas where topographically fixed oceanographic processes concentrate prey than it is for them to forage in areas where prey are both spatially and temporally unpredictable. Returning to predictably located feeding areas could be particularly advantageous during years of decreased food availability or at times during the breeding season when energetic demands associated with chick provisioning are elevated.

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