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Authors

Schneider, David Harrison, Nancy M Hunt, George L

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Variation in the Occurrence of Marine Birds at Fronts in the Bering Sea

David Schneider^a, Nancy M. Harrison^b and George L. Hunt, Jr^c

^aNewfoundland Institute for Cold Ocean Science, Memorial University, St. John's, Nfld, Canada A1B 3X7, ^bEcology and Evolutionary Biology, University of California, Irvine, CA 92717 U.S.A., and ^cEcology and Evolutionary Biology, University of California, Irvine, CA 92717 U.S.A.

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Topographically-induced flow gradients can concentrate seabird prey in several different ways, and are potentially important to marine birds in shelf ecosystems such as the south-eastern Bering Sea. We tested the hypothesis that attendance by seabirds was greater at fronts maintained by strong surface flow gradients than at fronts maintained by weak or intermittent surface flow gradients. An analysis of 62 crossings of flow gradients identified from temperature and salinity gradients showed that local increase in attendance was greater in areas of strong surface flow gradient than in an area of weak surface flow gradients. Attendance by marine birds depended on the strength of a flow gradient rather than on the presence or absence of a front.

Introduction

Marine birds live in a dynamic environment where flow gradients can increase the local concentration and production of marine organisms (Owen, 1981; Holligan, 1981). Flow gradients, which are defined as changes in water velocity in horizontal or vertical directions, can concentrate the prey of marine birds in at least four different ways. Convergent flow (downwelling) can increase the patchiness of vertically migrating prey such as myctophids (Olson & Backus, 1985) and jellyfish (Hamner & Schneider, 1986). Divergent flow (upwelling) can bring prey to the sea surface, where it can be captured by non-diving species. Coastal upwelling can increase subsurface concentration of negatively phototactic prey such as euphausiids (Simard *et al.*, 1986). Flow gradients may also maintain property gradients (' fronts ') to which nekton can respond directly. Temperature gradients, for example, can concentrate schooling nekton that prefer specific temperature ranges (Luka, 1978; Magnuson *et al.*, 1981).

Coarse-scale (1–100 km) flow gradients in shelf ecosystems are typically associated with topographic features (Csanady, 1982), and can be identified from gradients in temperature, salinity, or other properties of the water column. Over the south-eastern Bering Sea shelf, surface flow gradients are associated with changes in bottom topography near the 50-, 100-, and 170-m isobaths (Coachman, 1986). Flow gradients at the sea surface are strongly convergent near the 50-m isobath, intermittently convergent or divergent near the 170-m (shelf) break, and weakly convergent and divergent at the 100-m isobath. The location of surface flow gradients shifts in response to the wind, especially in deeper waters of the outer continental shelf. Flow gradients maintain cross-shelf temperature and salinity gradients that are typically strong at the surface in the vicinity of the 50- and 170-m isobaths and strong at the bottom near the 100-m isobath (Coachman, 1986).

Local increases in seabird abundance have been reported at a variety of physical features maintained by coarse-scale flow gradients, including current boundaries (Brown, 1979; Ainley & Jacobs, 1981), eddy boundaries (Haney, 1986), and water mass boundaries on continental shelves (Schneider, 1982; Kinder *et al.*, 1983; Haney & McGillivary, 1985). Fronts are maintained by flow gradients that differ in their surface expression, intensity, and persistence but little is known about the relation between bird abundance and frontal variability. Seasonal variation in the abundance of marine birds between Cape Hatteras and Cape Canaveral was associated with seasonal changes in the frequency and linear extent of mid-shelf fronts (Haney & McGillivary, 1985) but was not associated with seasonal variation in the strength of Gulf Stream eddies (Haney, 1986). Variation in seabird abundance has not been investigated in relation to spatial variation in the strength of flow gradients that maintain fronts. We hypothesize that there will be a greater abundance of birds in areas of strong surface-flow gradients (near the 50- and 170-m isobaths) than in areas of weaker surface flow gradients (near the 100-m isobath).

Previous analyses of habitat selection by marine birds have relied either on parametric methods, which may have a high Type I error for non-normally distributed data such as seabird counts, or have relied on non-parametric methods, which are relatively insensitive and may have high Type II error. We used Monte Carlo methods (Schreider, 1966) to obtain a distribution-free estimate of the Type I error of parametric analyses of cross-shelf differences in seabird abundance in the south-eastern Bering Sca.

Methods

Bird and physical data were recorded during repeated traverses of a single transect beginning on the continental slope $(54^{\circ}51'N, 167^{\circ}52'W)$ and extending 450 km northeastward toward Cape Newenham, in Bristol Bay (Coachman, 1986). Temperature and salinity measurements were obtained from CTD casts made at 25-km intervals along the transect. Seabird counts were made while travelling between CTD stations during daylight hours. All birds were recorded within 300 m of the ship, using a 90° sector from the bow to the side with the best visibility. Latitude and longitude were recorded at the start and stop of 10-min watches. To control for variation in ship speed each count was divided by the area scanned during each watch. Ship-following birds were excluded from calculations. Further details about the counting procedure and location can be found in Hunt *et al.* (1981) and Coachman (1986).

To estimate the location and direction of the flow gradient (low to high) in each crossing of the 50-, 100- and 170-m isobaths, we drew isopleths and then marked regions of strong lateral property gradients (bunched vertical isopleths) as shown in Figure 1. Salinity gradients were used except in those cases where thermal gradients were stronger. Property gradients are maintained by flow gradients, so the direction of the flow gradient was taken to be the same as the property gradient, i.e. negative running from an area of bunched vertical isopleths (a front) to an adjacent area of more widely spaced isopleths (Coachman, 1986). Seabird abundance was defined as the number of birds observed per unit area



Figure 1. Salinity profile along transect A in 1979. Transect begins at 54°51'N, 167°52'W and crosses north-eastward across the continental shelf.

scanned in a 300 m wide strip on one side of the ship. The cross-shelf difference in abundance d, at the spatial scale of the flow gradient was defined as:

$$d = (B - A)L^{-1} \tag{1}$$

where B is the number of seabirds observed during all 10-min counts in an area of bunched vertical isopleths, divided by the area scanned during these counts; A is the seabird abundance in an adjacent area of comparable extent, but with more widely spaced isopleths; L is the distance (km) between centres of the two areas being compared. Detection errors were assumed to be the same within each pair of adjacent blocks, A and B. The unit of measurement of differential abundance was (birds km⁻²) km⁻¹, abbreviated as birds km⁻³. A positive difference (d>0) indicates more birds at an identifiable flow gradient (front) than in an adjacent area. A negative difference indicates fewer birds at an identifiable flow gradient than in an adjacent area.

Surface-flow gradients are stronger near the 50- and 170-m isobaths than near the 100-m isobath (Coachman, 1986). The difference in bird abundance at the 50- and 170-m isobaths, averaged over all crossings, was therefore compared with the difference in abundance near the 100-m isobath, averaged over all crossings. The null hypothesis was:

$$H_0: \bar{d}_{50} + \bar{d}_{170} = 2\bar{d}_{100}$$

The alternative hypothesis for a one-tailed test was:

$$H_1: \overline{d}_{50} + \overline{d}_{170} > 2\overline{d}_{100}.$$

We also tested whether the mean difference over all crossing of identifiable flow gradients was greater than zero. The null hypothesis was:

$$H_0: d=0,$$



Figure 2. Differences in seabird abundance across coarse-scale flow gradients identified from property gradients.

where d is the difference in seabird abundance averaged over all crossings. The alternative hypothesis for a one-tailed test was:

$$H_2: \overline{d} > 0.$$

The data were considered to be accurate on an interval scale and so analysis of variance (Scheffe, 1959) was used to test hypotheses. Analysis of variance can detect small differences in seabird abundance but Type I error rate (erroneous rejection of the null hypothesis) can be high if the underlying assumptions for the analysis are not met. We used Monte Carlo methods (Schreider, 1966) to obtain a distribution-free estimate of the Type I error for each analysis of variance. The distribution-free estimate of the Type I error was obtained by randomizing the data to render the null hypothesis true, and then counting the number of times the null hypothesis was rejected by analysis of variance (at p = 0.05) in 100 trials. We used a binomial test (Siegal, 1956) to determine whether the observed number of rejections differed from the expected number, 5 out of 100. The parametric analysis was considered valid if the observed Type I error did not differ significantly from the expected rate, 5%. A Fortran subroutine (GGPER) from the IMSL Library (IMSL, 1982) was used to obtain random permutations of the values of B (average abundance in areas of bunched isopleths) and values of A (average abundance in adjacent areas) in each of the 100 trials.

Results

Temperature and salinity gradients, which are maintained by flow gradients, were identified at the expected locations near the 170-, 100-, and 50-m isobaths (Figure 1). Adequate seabird and physical data were available to calculate differences in abundance at 23 identifiable gradients near the 170-m isobath, 32 gradients near the 100-m isobath, and 7 gradients near the 50-m isobath. The total number of cases was 62, of which 32 were from 1981, 20 were from 1980, 6 were from 1979, and 4 were from 1978. The seasonal distribution of cases was 3 in March, 9 in April, 14 in May, 25 in June, 6 in July, and 5 in October. Northern Fulmar (*Fulmarus glacialis*) and Fork-tailed Storm Petrels (*Oceanodroma furcata*) accounted for most of the birds seen in deeper water of the outer shelf. Murres (*Uria* spp.) and shearwaters (*Puffinus tenuirostris* and *P. griseus*) accounted for most of the birds observed in shallower water inside the 100-m isobath.

A plot of all 62 cases showed that the largest positive differences in seabird abundance occurred near the 50-m isobath (Figure 2). The largest negative differences occurred on the seaward side of the 100-m isobath and landward of the 170-m isobath. The largest positive difference was 5.46 birds km⁻³; the largest negative difference was -4.97 birds km⁻³. Most of the remaining cases clustered around the mean value, which was 0.194 birds km⁻³.

Differential abundance of seabirds across regions of strong flow gradient exceeded differential abundance across regions of weak flow gradient. The mean difference near the 50- and 170-m isobaths, 0.327 birds km⁻³, was significantly greater than the mean difference near the 100-m isobath, 0.07 birds km⁻³ (F=4.69, p=0.017). The Type I error for this parametric test, based on 100 randomizations, was 9 out of 100 trials. This did not differ significantly from the expected rate of $5^{\circ}_{/0}$ (p=0.063, binomial test). The observed *F*-ratio for unrandomized data (F=4.69) was exceeded in 2 out of 100 trials, resulting in a distribution-free probability estimate (p=0.02) that was close to the parametric estimate (p=0.017).

When we looked at all fronts, rather than comparing areas of strong and weak flow gradient, we could not detect a significant increase in seabird abundance. The ratio of positive to negative differences was 36-to-26, which is statistically indistinguishable from a 1-to-1 ratio (p=0.13 binomial test). The mean difference in abundance across all fronts $(\overline{d}=+0.194 \text{ birds km}^{-3})$ was statistically indistinguishable from zero (F=1.1, p=0.148). The Type I error for this parametric test, based on repeated randomizations of the data, was 4 out of 100 trials. This did not differ significantly from the expected error rate of 5°_{0} (p=0.436, binomial test). The observed *F*-ratio for unrandomized data (F=1.1) was exceeded in 18 out of the 100 trials, resulting in a distribution-free probability estimate (p=0.18) that was close to the parametric estimate (p=0.148).

Discussion

On average, the abundance of marine birds at identifiable fronts did not exceed abundance in adjacent areas of the ocean. This result is consistent with distributional studies from the entire south-eastern Bering Sea. Cartographic presentations of seabird abundance at a temporal resolution of three months and spatial resolutions of 55 km (Hunt *et al.*, 1981) or 20 km (Gould *et al.*, 1982) do not show bands of high bird density along the 50-, 100-, or 170-m isobaths.

Seabird abundance did increase in areas of strong flow gradient, even though the average difference across all fronts was not significant. This led us to hypothesize that crossfrontal differences in seabird abundance might be a direct function of the strength of the flow gradient maintaining the front. In formal terms the model was:

$$d = mG \tag{2}$$

where *m* is a coefficient relating the differential abundance of seabirds, *d*, to the flow gradient *G* when *d* is computed at the same spatial scale as the flow gradient. As an index of the flow gradient *G* we used the reciprocal of the length scale of salinity and temperature gradients, measured as the reciprocal of the distance $L_{\rm B}$ across the area of bunched vertical isopleths (Figure 1). The model cannot be evaluated directly by regression because *d* is computed on the basis of $L_{\rm B}$ and hence variation in $L_{\rm B}$ contributes to variation in the measured differential in bird abundance, *d*. However, by defining a new variable

D = dL

we obtain an expression

$$D = m' L_{\rm B}^{-1} L \tag{4}$$

$$D = m' L_{\rm B}^{-1} (L_{\rm B} + L_{\rm A})/2 \tag{5}$$

that can be evaluated by regression. Model parameters, as estimated by regression, were

$$D = -14.7 + 11.8 L_{\rm B}^{-1} (L_{\rm B} + L_{\rm A})$$
(6)

The slope of the regression line differed significantly from zero (t=4.68, df=60, p=0.0001). The intercept was not significant (t=-1.71, df=60, p=0.09) and so with some further rearrangement the resultant model of cross-frontal difference in seabird abundance is

$$d = 23.5 L_{\rm B}^{-1} \tag{7}$$

In assessing this model it is important to note that cross-shelf differences in seabird abundance were not compared directly to flow gradients, which were hypothesized to concentrate seabird prey and reduce foraging costs. The spatial scale of salinity and temperature gradients was used as an index of the strength of the flow because flow gradients are difficult to measure directly, because property gradients are maintained by flow gradients, and because the relation between a property gradient and a flow gradient can be modelled successfully in some circumstances (Csanady, 1982). Confirmation of the importance of coarse-scale flow gradients to marine birds will require direct measurement of rates of food extraction in relation to flow-induced changes in the local density and production of prey. These measurements need to be made using the appropriate time and space scales.

We were unable to determine whether the birds we observed were actively feeding in areas of strong flow gradient. Surveys along the study transect were completed in less than four days to minimize temporal variation, and this precluded extended observation of feeding behaviour. Duffy (1983) found that, at least in the tropics, aggregated seabirds attack prey more frequently than non-aggregated birds. The relation between attack rate and aggregation needs to be measured in boreal seabirds.

Coarse-scale aggregations of marine birds are associated with coarse aggregations of prey (Schneider & Piatt, 1986), but the dynamics of these aggregations, including rates of formation and dispersal, have not been investigated. The temporal and spatial scale of seabird aggregations appear to be linked (Hunt & Schneider, 1986). Fine-scale aggregations (<1 km) typically form and disperse in a matter of an hour or less (Hoffman *et al.*, 1981; Duffy, 1983). Coarse-scale aggregations of actively feeding murres persist over periods of 1–10 h in the vicinity of breeding colonies in the Bering Sea and on the western Grand Banks (Schneider, unpubl.). Macro-scale aggregations (100-1000 km) may persist for weeks or months. The temporal scale of seabird aggregations is, in general, much less than the temporal scale of physical features of comparable extent. The contributions of flight capacity (in excess of 1 km min⁻¹) and long-distance orientation (thousands of km over several days in some species) to the formation of seabird aggregations need to be measured in relation to physical processes that can concentrate seabird prey.

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