Spatial autocorrelation in marine birds

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All marine organisms exhibit some degree of spatial autocorrelation, which is the tendency for high (or low) densities to occur in proximity, rather than at random in the ocean. Autocorrelation occurs at scales ranging from the length of the organism to thousands of kilometres. Autocorrelation results from a wide variety of mechanisms, many of which act at characteristic scales. Consequently, some insight into causal mechanisms can be obtained from exploratory analysis of the scale and intensity of autocorrelation of abundance or behaviour, and the scale and intensity (coherence) of cross-correlation with environmental variables such as water temperature or prey abundance. This paper uses seabird counts along extended transects to illustrate standard measures of autocorrelation and cross-correlation. A brief discussion of exploratory and confirmatory analysis of autocorrelated data on marine birds follows.

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Intuitive measures of autocorrelation

Prior to 1980, measurement of seabird abundance and behaviour occurred almost entirely at stations with fixed coordinates, separated by large distances. The unit of measurement was a count standardized by time, by length of a strip transect, or by area of a strip transect (Tasker et al. 1984). The method was well suited to large scale surveys (e.g. Shuntov 1974; Brown et al. 1975), which necessarily sacrificed information on smaller scale heterogeneity (Devillers 1978) in the interests of observer alertness. Through a fortunate circumstance I was able to make spatially continuous counts along hundreds of kilometres of ocean in conjunction with PROBES, a multi-disciplinary investigation of circulation and biological production in the southeastern Bering Sea. The fortunate circumstance was the sampling design of PROBES, which consisted of measurements at stations separated by 25 km along a 500 km transect, running from the edge of the continental shelf northeastward toward the coast. By counting continuously between stations, I was able to obtain spatially (though not temporally) continuous counts along the hundred or more kilometres that the ship traversed during the long daylight hours of mid-summer in the Bering Sea.

Of course, I soon learned what many previous observers must have noticed, which is that one can expect to see many birds ahead if one sees many birds during the present count, and conversely, few birds ahead if few birds are currently in sight. This meant that one had to exert extra effort when counts were low, the expectation of few birds ahead tending to re-inforce itself through relaxation of attention.

After two traverses of the PROBES line in late May 1980, it also became clear that systematic increases and decreases in bird abundance occurred over distances of tens of kilometres, a pattern that had not been previously reported in marine birds. The pattern in the Bering Sea was repeatable from year to year. Fig. 1 shows the July 1982 distribution of birds along the same transect that was traversed in May 1980. Coarse-scale (1 to 100 km) aggregations have now been reported in marine ecosystems as diverse as the California Current (Briggs et al. 1984), the Benguela Current (Schneider & Duffy 1985), the Labrador Current (Schneider & Piatt 1986), and the Agulhas Current (Abrams & Lutjeharms 1988).

The Bering Sea transect could not be analysed by standard techniques for continuous data because of breaks in the series during nighttime transit between stations. The solution that I adopted, working from analogy with the structure of much smaller aggregations (Hoffman et al. 1981), was to assume a characteristic structure for these aggregations – attenuation in density with increasing distance from some focal point. The analytic procedure was to construct filters of varying widths, each with the peaked shape of a hypothetical bird aggregation, slide each filter along the transect, and measure fit of the data to the

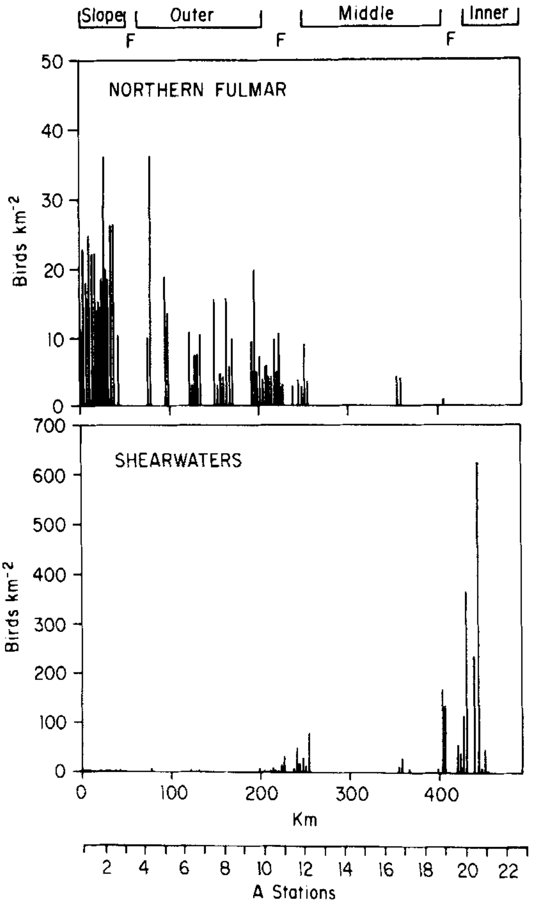

Fig. 1. Abundance of fulmars *Fulmarus glacialis* and dark-bellied shearwaters, primarily *Puffinus tenuirostris*, along a 534 km transect, running from the shelf break northeastward across the Bering Sea toward Cape Newenham. Transect begun 26 July 1982, completed 28 July 1982. Redrawn from Schneider, Hunt & Harrison (1986).

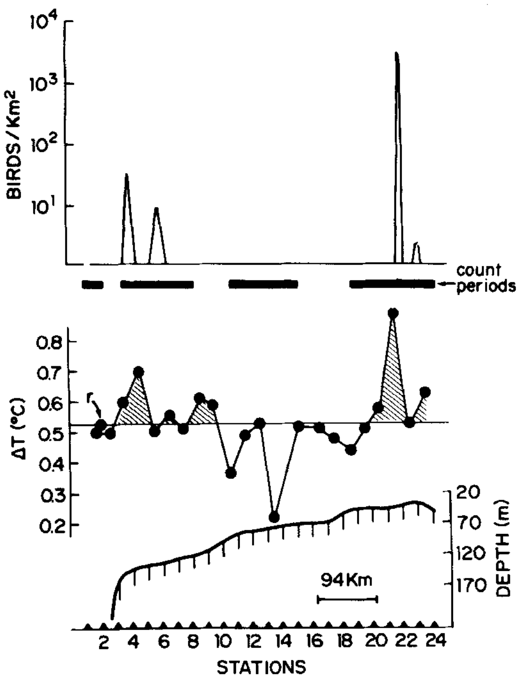

Fig. 2. Location of structured aggregations along same transect line as shown in Fig. 1. Transect begun 31 May 1981, completed 3 June 1981. Delta-t is a measure of change in thermal structure between adjacent stations. Redrawn from Schneider (1982).

filter at successive positions along the line. The analysis (Schneider 1982) showed good fit (r^2 ranging from 77% to 95%) at two fronts, poor fit (r^2 less than 77%) along the rest of the transect. This result meant that ten-minute counts (each approximately 3 km long) were autocorrelated at lags (separations) ranging from 1 (adjacent counts) to 3 (half the observed chord length of an aggregation) near the two fronts. A simple Monte Carlo analysis, using random rearrangements of the observed ten-minute counts, showed that erroneous identification of structured aggregations (Type I error) by this filtering procedure was small (<5%). Fig. 2 shows the location of structured aggregations of seabirds along the transect in June 1981.

One extension of this analytic approach is to use a wider variety of filters, guided perhaps by a formal or informal model of patch shape. Abrams & Lutjeharms (1988) used bell-shaped (Gaussian) filters centred on areas of high SST gradient to examine the relation between seabird abundance and fronts. Abrams used a routine from the BMDP package, a considerable savings in effort over the hand computations used in the analysis of the Bering Sea data. Still more sophisticated approaches can be found in the literature on digital filtering (e.g. Mendel 1987).

A related approach, developed by Cliff & Ord (1973), is to test whether observed abundances fit a hypothetical pattern of association between counts, whether adjacent or not. This method requires specification of a join structure – some *a priori* pattern of relatedness in space against which to test the data. This technique has proved most useful in the analysis of discrete geographic units of unequal size (such as counties) and readily specified join structure (such as roads linking counties).

The spatial scale of autocorrelation

In marine ecosystems one rarely has any basis for specifying a join structure, but one often has enough data to measure the strength of autocorrelation between counts as a function of distance between counts. In oceanography one needs to know the spatial scale of a phenomenon before one can proceed to estimating rates or investigate underlying processes. One way of determining scale is to ask whether the values of a variable are associated with previous values and over what distances. A correlation coefficient (e.g. the familiar Pearson coefficient, r) can be calculated at increasingly large lags s to produce a vector of autocorrelations r(s). These numbers can be plotted against lag to obtain a correlogram. Sokal (1979) discusses the use and interpretation of correlograms in ecological contexts. One use of the correlogram is to determine how widely spaced counts need to be in order to be considered spatially independent. One should use separations at which r(s) lies 'near enough' to zero.

Correlograms of ecological data often show association at small lags, decaying to negligible association at larger lags. If such is the case, r(s) can be modeled using the exponential decay function:

$$r(s) = e^{-ks} \qquad (1)$$

where r(s) is the autocorrelation at lag s, e is the base of natural logarithms, and k is a constant decay rate to be estimated from the data. When s equals zero, r(s) equals one.

An appropriate autocorrelation function can be used to filter out autocorrelation within a series (Box & Jenkins 1976), allowing accurate tests of treatment effects (e.g. 'More birds here than there?') with statistical control for autocorrelation of contiguous or closely spaced counts. This is a solution to the problem of 'pseudo-replication' (Hurlburt 1984), if one can estimate the autocorrelation function.

How much autocorrelation can be expected in counts of marine birds along extended transects? If strong autocorrelation occurs in distributional data, then we need to worry about its effects on our analyses, and we can expect considerable improvement in our analyses by using statistical control to remove the effects of autocorrelation. Intuitively we might anticipate autocorrelation of marine bird counts at separations of tens of metres, because individuals of many species move toward other birds to form loose aggregations at this scale. The same observation leads us to anticipate less autocorrelation at separations beyond the limits of visual contact. These limits might vary from tens of meters for birds sitting on the water to several kilometres for large-bodied soaring species. This observation on seabird behaviour suggests that equation (1) might hold true for marine birds at separations ranging from tens to thousands of metres.

An analysis of autocorrelation was carried out with data on the abundance of gliding species along a transect running westward across the Labrador Shelf, through a narrow pass with strong tidal currents (Gray Strait) and then out into Hudson Strait (Fig. 3). Turbulence in this passage reaches extraordinary levels. Turbulence in Gray Strait was evident in the motion of the research vessel (CSS 'Hudson' c. 70 m in length), which lurched laterally as it steamed at 11 knots relative to the water. Boils of water as large as the ship rose to the surface around and under the ship as it passed through the strait. Birds were observed hovering around these boils, which may have been bringing food to the surface. Marine bird concentrations have been reported in straits with turbulent flow in the Gulf of Maine (Braune & Gaskin 1982; Mercier & Gaskin 1985), on the west coast of Scotland (Bourne & Harris 1979) and in the Bering Sea (Gould et al. 1982). Marine

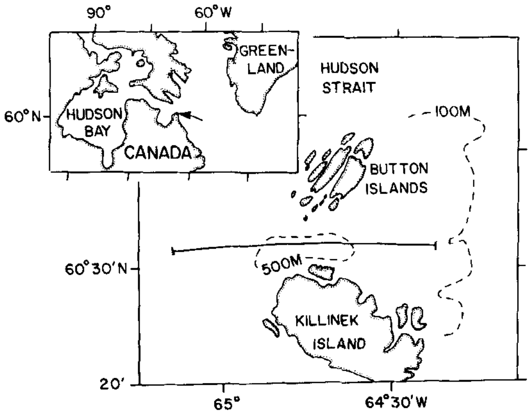

Fig. 3. Location of 42.9 km transect through Gray Strait.

Table 1. Number of birds observed along a transect through Gray Strait on 18 September 1985. Transect was 42.9 km long, starting at 1311 hrs. GMT, ending at 1440 hrs. GMT.

Species	On water	Flying
F. glacialis	234	327
Larus hyperboreus	0	2
R. tridactyla	8	113

bird abundance in areas of high turbulence, relative to adjacent areas, has not been quantified.

Counts through Gray Strait were made on one side of the ship out to the limit of visibility, which was 100 m in foggy conditions. Table 1 shows the species and behaviour of all birds observed along the transect. Fig. 4 shows counts of the three most abundant groups – fulmars *Fulmarus glacialis* in the air, fulmars on the water and kittiwakes *Rissa tridactyla* in the air. Fig. 5 shows the autocorrelation of counts at lags from s = 0 to s = 100 (2 km). Flying fulmars were more strongly autocorrelated than fulmars on the water and flying kittiwakes. Fulmars in the air showed a pattern of autocorrelation at lags close to multiples of 5 (100 m). This is approximately the diameter of large boils of water upwelling to the surface in the strait, so one interpretation is that fulmars were aggregating in relation to these physical structures.

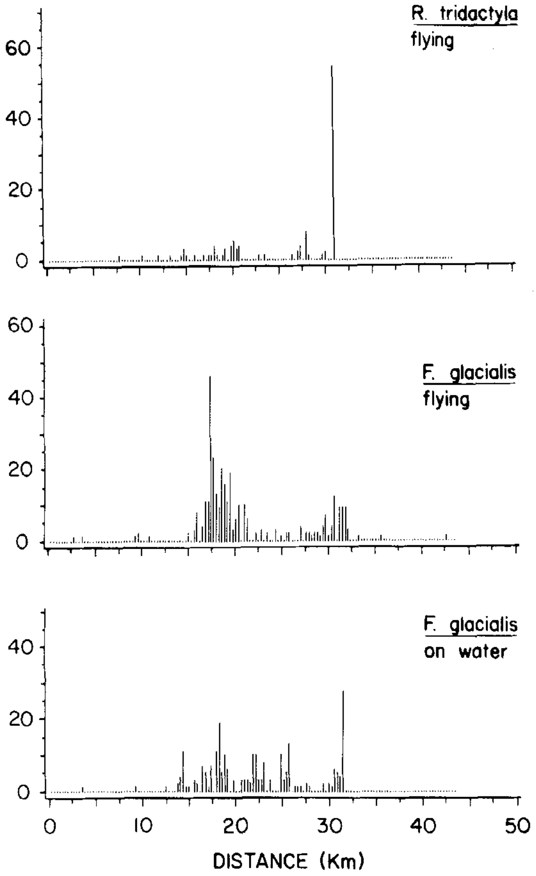

Fig. 4. Counts of flying birds (fulmars and kittiwakes) and birds on the water (fulmars) along Gray Strait transect. Counting interval of L = 0.3 km used to present data.

None of the three analyses showed local autocorrelation decaying to negligible correlation at distances beyond the limit of visibility. Significant autocorrelation occurred at some lags, but no consistent pattern emerged in comparing one species across several transects, or in comparing several species along the same transect. Autocorrelation was weak ($r(s) < 0.3$) in the Gray Strait data. The spatial resolution was 20 m, so it will be interesting to see if weak autocorrelation proves generally true of marine bird counts taken at different spatial resolutions.

Rather than looking at correlation as a function of increasing lag, one can divide continuous data into a sequence of counts in contiguous intervals, beginning at the interval of minimum spatial resolution and proceeding to larger intervals. If seabird counts are recorded directly on paper while underway, the minimum practical recording interval is 1 minute, corresponding to a spatial resolution of approximately 300 m at a ship speed of 10 knots (c. 5 m s^{-1}). With a computer one can record sightings at temporal resolutions of a second or less to obtain spatial resolutions of 10 m or less at ship speeds of ten knots. The traditional resolution used in seabird work has been 10 minutes, or roughly 3 km at ship speeds of 10 knots. One consideration in choosing the minimum resolution interval is that more information can be extracted from high resolution than from lower resolution data. Another consideration is that one can always construct lower resolution data (e.g. a sequence of ten-minute counts) from higher resolution data (e.g. a sequence of one minute counts) but not vice versa.

A natural step at this point is to ask what happens if one changes the recording interval, either through better instrumental resolution, or as a way of looking at the data. The mean (per count) at any given recording interval can be calculated from the mean obtained at any other

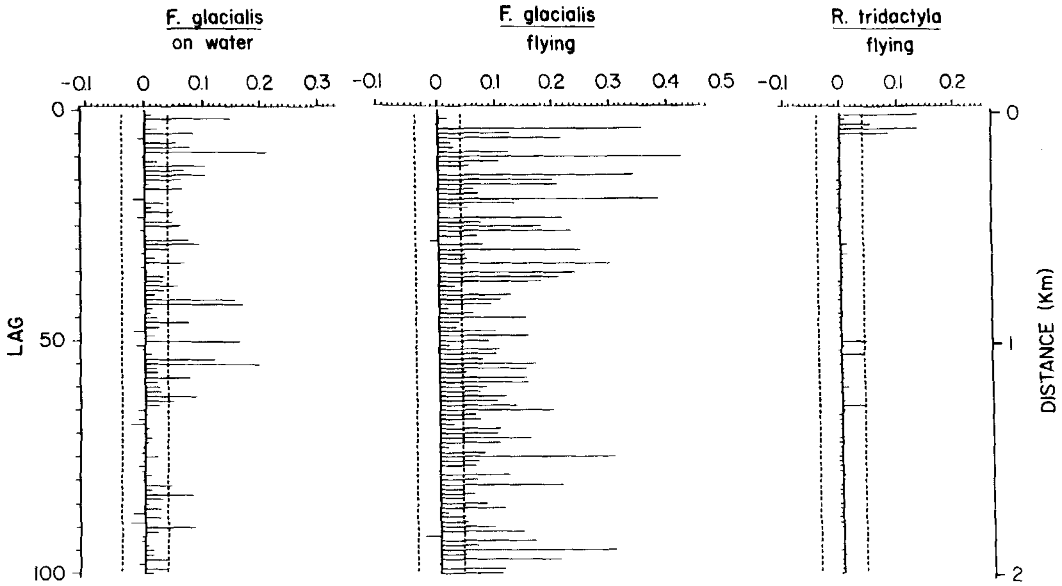

Fig. 5. Autocorrelation of flying birds (fulmars and kittiwakes) and birds on the water (fulmars) along Gray Strait transect. Dotted lines are 95% confidence intervals.

recording interval. Let $N_i[L]$ denote the observed count in the i^{th} interval of length L, and let $\bar{N}[L]$ denote the mean of the $N_i[L]$ counts. Explicitly,

$$\bar{N}[L] = \frac{1}{m}\sum_{i=1}^{m} N_i[L] \qquad (2)$$

where m is the number of intervals of length L in a transect of length T. If L_0 is the length of the minimum observable interval, then it can be shown that

$$\bar{N}[L_0] = \frac{1}{n}\bar{N}[L] \qquad (3)$$

where $n = L/L_0$, the number of minimum resolution intervals within an interval of length L. Quantities L, L_0 and T have the same units, such as kilometres. Equation (2) states that from any set of observations $N_i[L]$, one can infer the mean count at intervals of any other length.

What about the variance calculated at scale L, $\tilde{N}^2[L]$? This quantity, like $\bar{N}[L]$, is a function of L:

$$\frac{\tilde{N}^2[L]}{n} = \mathrm{Var}(N_i) \quad i = 1 \text{ to } TL^{-1} \qquad (4)$$

This quantity, unlike the mean $\bar{N}[L]$, cannot be rescaled to a constant. However, we do find that we have computed a familiar quantity, the mean squared variance among groups, MS_{among}:

$$\mathrm{Var}(N_i) = \frac{1}{m-1}\sum_{i=1}^{m}(\bar{N}_i[L] - \bar{N}[L_0])^2 \qquad (5)$$

To see what happens when we change interval length L, we can begin with a transect of length T marked off into intervals of minimum resolution, L_0, then calculate the variance at this scale, $\tilde{N}^2[L_0]$. We can then group adjacent intervals into pairs to obtain intervals of length $L = 2L_0$. The variance at this scale, $\tilde{N}^2[2L_0]$ is:

$$\tilde{N}^2[2] = \mathrm{Var}(N_i^{left} + N_i^{right})\; i = 1 \text{ to } TL^{-1} \qquad (6)$$

where N_i^{left} symbolizes counts on the left side of pairs and N_i^{right} symbolizes counts on the right side of pairs. Consequently,

$$\tilde{N}^2[2L_0] = \mathrm{Var}(N_i^{left}) + \mathrm{Var}(N_i^{right}) + 2r_{lr}\,\mathrm{Var}(N_i^{left})\,\mathrm{Var}(N_i^{right}) \qquad (7)$$

where r_{lr} is the correlation between adjacent (left and right) subintervals. Dividing this equation by n, we obtain:

$$MS_{among} = MS_{within} + 2r_{lr}n^{-1}\mathrm{Var}(N_i^{left})\mathrm{Var}(N_i^{right}) \qquad (8)$$

From this equation we see that if adjacent subintervals (left and right) are not correlated, then r_{lr} will be zero and the variance at the scale of intervals (MS_{among}) will be the same as the variance at the scale of subintervals (MS_{within}). If adjacent subintervals are positively correlated, then variance at the scale of intervals (MS_{among}) will exceed variance at the scale of subintervals (MS_{within}), depending on the strength of correlation, r_{lr}. If adjacent subintervals are negatively correlated, then the variance at the scale of intervals will be less than the variance at the scale of subintervals. This can be generalized to larger subintervals by grouping adjacent pairs to obtain intervals of $L = 4L_0$, grouping these pairs to obtain intervals of $L = 8L_0$, etc.

We obtain a similar result if we use the variance-to-mean ratio at successively larger intervals because:

$$\begin{aligned} I'[L] &= \frac{\tilde{N}^2[L]}{\bar{N}[L]} \\ &= \frac{\tilde{N}^2[L]}{n} \cdot \bar{N}[L_0]^{-1} \\ &= MS_{among} \cdot \bar{N}[L_0]^{-1} \qquad (9) \end{aligned}$$

Scaling of the variance to the mean in this fashion produces a statistic that, in theory, will not vary with change in scale L as long as counts are independent (not autocorrelated). In practice, some systematic change in I'[L] with change in L can occur because of increase in bias (Reed 1983), as the number of intervals ($m = TL^{-1}$) decreases (L increases). In working with seabird counts, my experience has been that this problem is serious enough to preclude attempts to estimate the true value of I'[L], but not serious enough to preclude plotting I'[L] against L to look at scale-dependent structure in abundance of birds along transects. Not all measures of variability have the property of being theoretically independent of L if counts are independent (uncorrelated with themselves). The measure of variability advocated by Green (1979), for example, varies with L when random numbers are used.

To obtain an idea of the spatial scale at which variability is concentrated, one can plot the variance among groups against the length of the counting interval, L. One expects variability to be unchanged if counts are independent (not autocorrelated). One expects variability to increase until one reaches the interval roughly equal to the chord length of a patch. This is the contiguous quadrat method of Greig-Smith (1952), which was modified for line transect by Kershaw (1957). The contiguous grouping method has been used to examine the scale of variability of seabird counts (Schneider & Duffy 1985) and to show that correlation between alcid abundance and capelin prey changes with spatial scale (Schneider & Piatt 1986). Fig. 6 shows the results of contiguous grouping of the kittiwake data from the Gray Strait transect. More birds were observed in the strait than on either side; this shows as an increase in variability at grouping intervals of more than half an hour, equivalent to interval lengths of 8 km or more.

We began by thinking about change in variability with increase in the length of the counting interval. We then plotted a measure of variability, the variance-to-mean ratio, among contiguous intervals. The abscissa is the bin size, or frame size: 1 minute count, 5 minute count, 10 minute count, 20 minute count, etc. (Fig. 6). We can think about the abscissa of this plot in another way. It is a measure of the frequency of counts along a transect of fixed length. For a 16 km transect we have 1/16, 2/16, 4/16, etc. What we have done is to have plotted variability against frequency, with high frequencies on the left, low frequencies on the right. The jargon term for this operation is 'working in the frequency domain'.

The contiguous grouping method (where statistics are calculated in the frequency domain) is related to spatial autocorrelation (which is calculated as a function of separation) through the

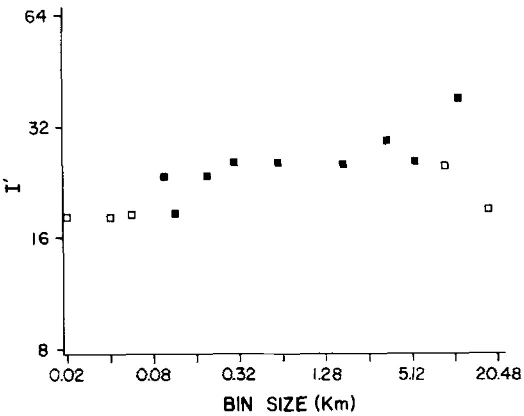

Fig. 6. Variability, as measured by the variance-to-mean ratio I'[L], of kittiwakes on Gray Strait transect. L is grouping interval.

periodogram I(w), which uses periodic functions to describe variability as a function of the frequency of grouping (w) within the set of data. The contiguous grouping method of Greig-Smith results in a periodogram constructed from square waves (Ripley 1978). The correlogram r(s) and the periodogram I(w) are related via the Fourier transform (cf. Ripley 1981).

After obtaining a plot of variability as a function of scale, one naturally asks whether the plot can be reduced to some simple functional expression, in much the same way that one approached the correlogram. The statistical literature warns us, however, that the periodogram I(w) is a poor estimator of the underlying continuous function, which is called the spectral density. Better results can be obtained (given certain conditions on the data) by using a filter to compute a smoothed estimate of the spectral density. One can also estimate the cross-spectra between two series to obtain the coherence h(w), which is a measure of association between the two series at frequency w. Much of the art in performing this sort of analysis comes in choosing the filter. The result, a spectral analysis, is a sophisticated version of the contiguous grouping method of Greig-Smith (Ripley 1978). In a comparison of several different methods of analysing transect data, Ripley (1978) found that spectral analysis seems to be the most reliable method for detecting a pattern. Platt & Denman (1975) discuss the use of spectral analysis in ecology. An extensive catalogue of other spatial methods can be found in Upton & Fingleton (1985). A mathematical review of spatial methods can be found in Ripley (1981). Diggle (1983) covers tests of randomness in spatial data and the construction of stochastic models.

Exploratory and confirmatory analysis

In the abstract, spectral analysis and lagged autocorrelation analysis are closely related. In practice, spectral analysis can usually tell us more about the data at hand than analysis on the autocorrelation side (Tukey 1970). To illustrate this point, we can compare autocorrelation analyses of the Gray Strait data to spectral analyses of the same data. Fig. 7 shows the spectral density of counts of fulmars on the water, fulmars in the air and kittiwakes in the air. In the plot of the data (Fig. 4) we see large scale variability in abundance associated with passage into and out of Gray Strait. We can see that substantial variability exists at smaller scales, but we cannot compare species with respect to this variability at these scales. Autocorrelation analysis (Fig. 5) shows that fulmars and kittiwakes differ in patterns of smaller scale variability and that fulmars in the water differ from flying birds with respect to smaller scale variability. The plot of autocorrelations (Fig. 5) gives no sense of the larger scale variability in abundance, or how this compares with the smaller scale variability. We could plot the autocorrelations at lags up to half the length of the series, but such a plot, with over 1,000 correlation coefficients, is not an informative way of summarizing the data for examination. In Fig. 7 we see that all three groups – flying kittiwakes, flying fulmars, and sitting fulmars – exhibit more variability at spatial scales greater than 1 km than at smaller scales. We also see a second concentration of variability at scales on the order of 100 m in flying kittiwakes and fulmars, but not in fulmars on the water. At the smallest scale, less than 50 m, we see a concentration of variability in fulmars, both on the water and in the air. These patterns are not evident in the autocorrelation analyses, which are less effective at summarizing the variability in data through a range of scales.

An interpretation of the Gray Strait transect can now be offered along the following lines: Two surface feeding species, kittiwakes and fulmars, were found at higher concentrations in turbulent waters of the strait than in adjacent, less turbulent

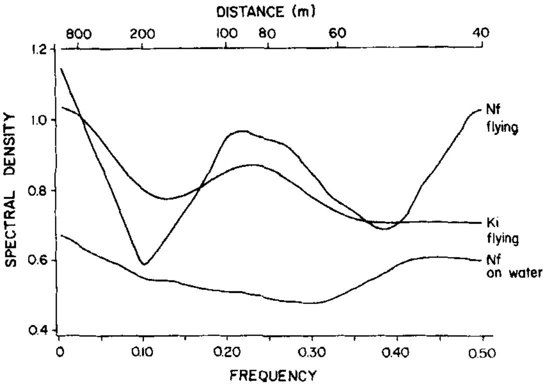

Fig. 7. Spectral analysis of flying birds (fulmars and kittiwakes) and birds on the water (fulmars) observed along Gray Strait transect. The smoothing window (bandwidth = 0.2) was triangular.

water. In addition, flying kittiwakes and fulmars showed spatial variability at the scale of large boils of water rising to the surface. Fulmars were abundant on the water, which suggests that birds were feeding and that the boils were bringing food to the surface. Fulmars on the water did not retain the same spatial structure as birds in the air, possibly due to passive transport of birds toward convergences at the edge of boils. This interpretation focuses on interactions between predators and prey in relation to the physical structure of the environment rather than on interactions between groups of birds. Cross-spectral analysis showed a positive association between each of the three groups at spatial scales greater than 1 km, no association (positive or negative) between any of the three groups at smaller spatial scales. Interactions between species do not appear to be an important source of variation in the abundance of kittiwakes and fulmars along this transect.

This analysis illustrates two related ideas. The first is that we need to distinguish between an exploratory approach and a confirmatory approach to data. Exploratory analysis, such as the Gray Strait study, is a matter of discovering what the data have to tell us. Confirmatory analysis, such as the identification of structured aggregations along the PROBES lines, is a matter of circumscribing what we can say with certainty. In this latter analysis the data were not used to construct the model, which was developed from prior surveys of the transect. In the Gray Strait analysis we could have used confirmatory procedures to test the *a priori* expectation of more birds in the strait than in adjacent waters. However, analysis of the smaller scale variability was entirely exploratory, with concepts being developed from investigation of the data at hand.

Related to this distinction between exploratory and confirmatory analysis is the second idea, which is that some techniques work better in exploratory than in confirmatory settings. Spectral analyses and factor analyses are good examples of techniques that work well in exploratory situations. We also have a large arsenal of confirmatory techniques, such as model fitting, that functions much better as confirmatory than as exploratory techniques. The idea of exploratory analysis, the attitude that this is a legitimate part of data analysis and the idea that some methods are better than others for exploring data have been elaborated by Tukey (1986).

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