

Scale-dependent spatial variance patterns and correlations of seabirds and prey in the southeastern Bering Sea as revealed by spectral analysis

Elizabeth A. Logerwell, Roger P. Hewitt and David A. Demer

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Uni- and bivariate spectral analyses of the spatial distribution of thick-billed murres *Uria lomvia* and acoustic estimates of prey biomass in the southeastern Bering Sea were used to examine the spatial variance patterns of a predator and its prey at multiple spatial scales. Power, phase and coherency spectra from individual transects, as well as those averaged over all transects, were examined. The average spectra, representing a temporal scale of months, showed that murres and prey had similar spatial variance patterns and were positively correlated over the range of spatial scales studied. The individual spectra, representing a temporal scale of hours, showed several patterns that were not evident in the average spectra. In particular, the transect-level analyses showed that the correlation between murres and prey was poor at spatial scales where prey variance was relatively low. This result suggests a new hypothesis to explain poor small-scale correlations between consumers and resources: resource distribution is relatively uniform at small scales resulting in only a slight increase in foraging return for consumers showing an aggregative response at these scales. The differences among spatial scales and between the average and individual spectra illustrate how ecological patterns can vary with temporal and spatial scale.

E. A. Logerwell, *Ecology and Evolutionary Biology, Univ. of California, Irvine, CA 92697-2525, USA (present address: Southwest Fisheries Center, 8604 La Jolla Shores Dr., La Jolla, CA 92037, USA)*. – R. P. Hewitt and D. A. Demer, *Southwest Fisheries Science Center, 8604 La Jolla Shores Dr., La Jolla, CA 92037, USA*.

Investigators are becoming increasingly aware of scale-dependent patterns in ecological systems. For example, spatial variation in plant and animal abundance (Ripley 1978, Greig-Smith 1979, Schneider and Duffy 1985, Schneider and Piatt 1986, Ludwig and Cornelius 1987, Briggs et al. 1988, Pickney and Sandulli 1990), the distribution of consumers relative to resources (Rotenberry and Wiens 1980, Wiens and Rotenberry 1981, Schneider and Piatt 1986, Wiens et al. 1986, Morris 1987, Heinemann et al. 1989, Hunt et al. 1990, Piatt 1990, Hunt 1991, Hunt et al. 1992, Brown and Morgan 1995) and the distribution of competing species (Sherry and Holmes 1988) have been shown to vary with mea-

surement scale. Thus, caution should be used in interpreting analyses at a single scale because they may not illustrate the important patterns. On the other hand, a multiscale analysis can illustrate at what scale or scales species are likely to interact and whether the interactions vary with scale (Wiens 1989). We conducted a multiscale investigation using spectral analysis to examine the scale-dependence of: 1) spatial variation of predator and prey abundance, and 2) spatial correlation between predators and prey.

Spectral analysis allows for the investigation of predator and prey distributions at multiple scales simultaneously (Platt and Denman 1975). For instance, the

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application of univariate spectral analysis to spatial (transect) data results in estimates of spatial variation (or patchiness) over a wide range of measurement scales (Jenkins and Watts 1968, Platt and Denman 1975, Chatfield 1984). The procedure involves fitting the original data series (along a transect) to sine and cosine waves at different frequencies (the inverse of measurement scale). Plots of spectral density, a measure of spatial variance, versus frequency are then produced that show how the variance is partitioned among the range of frequencies. A peak in spectral density indicates the scale at which organisms show particularly high spatial variance and thus may represent a scale of natural aggregation (Greig-Smith 1983). Changes in the slope of spectral density versus scale indicate transitions between spatial variance patterns that could similarly result from the formation of aggregations (Mandelbrot 1982, Horne and Schneider 1997).

Bivariate spectral analysis results in phase and coherency spectra that together describe the correlation between two variables, such as the abundance of predators and prey, as a function of measurement scale (Jenkins and Watts 1968, Platt and Denman 1975, Chatfield 1984). Squared coherency is analogous to the coefficient of determination in regression analysis and thus measures the strength of the correlation. The phase spectrum measures the amount that one data series lags or leads another data series at each measurement scale. In this way the phase measures the sign of the correlation, in-phase series (phase between -90° and $+90^\circ$) are positively correlated whereas out-of-phase series (phase $< -90^\circ$ or $> +90^\circ$) are negatively correlated. If predators are responding to the spatial distribution of prey then the expectation is that the bivariate spectra will be in phase with non-zero coherency.

We used uni- and bivariate spectral analysis of the spatial distribution of thick-billed murres *Uria lomvia* and acoustic estimates of prey biomass in the southeastern Bering Sea to examine the spatial variance patterns of and the correlations between a predator and its prey at multiple spatial scales. We examined the spectra for individual transects and we calculated mean spectra over all transects surveyed during the two years of the study. The average spectra increased the temporal scale of our study to several months, and allowed for comparisons with patterns occurring at the smaller temporal scale of individual transects, which were surveyed in a few hours.

Methods

Field methods

Data on the distribution of thick-billed murres and acoustic estimates of prey biomass were collected from

2 to 22 September 1994 and 10 to 25 September 1995 during the Fisheries Oceanographic Cooperative Investigations (Alaska Fisheries Center, National Marine Fisheries Service) in the southeastern Bering Sea (Fig. 1). Ten transects were surveyed in 1994. Five transects were surveyed in 1995, primarily in the vicinity of the Pribilof Islands. Transects ranged from 60 to 150 km in length. Thick-billed murres are the most numerous seabirds in the study area, with a breeding population of around 1.5 million on St. George Island (Pribilof Islands) (Sowls et al. 1978). Data on the distribution of thick-billed murres were collected by counting birds within a 300-m band transect to one side of the ship whenever underway. Counts of birds and data on their behavior (i.e., flying, feeding or sitting on the water) were entered into a field computer which assigned a time to each entry. The time, position, course and speed of the ship were entered into the computer every 30 min. or whenever the ship changed course or speed. This information was then used to calculate the position of all bird observations.

To investigate predator-prey relationships, acoustic measurements of prey biomass were conducted simultaneously with seabird observations. The diet of thick-billed murres around the Pribilof Islands consists of juvenile fish, and large zooplankton such as euphausiids and amphipods (Hunt et al. 1981, Decker et al. 1995, Decker and Hunt 1996). Acoustic estimates of prey were based on measurements of volume backscattering strength, made using a hull-mounted 120 kHz split-beam transducer and a Simrad EK500 echosounder. Acoustic data were indexed by time and ship's position. See Hewitt and Demer (1993) for detailed description of acoustic methods.

Analysis

Echograms were generated from the acoustic data set and interpreted with respect to potential prey. Volume backscattering was integrated from 10 m depth to 1 m above the bottom, or to a maximum depth of 150 m, and averaged over 370 m distance intervals (Hewitt and Demer 1993). Thick-billed murres have been observed to make foraging dives to a maximum depth of 153 m (Burger 1990), hence the 150 m depth maximum for the integration. The relationship between integrated volume backscattering strength and vertically integrated biomass is dependent on species composition of the scattering assemblage, the density and sound speed contrasts and body orientation of individual scatterers, and the number of individuals per unit area of sea surface. For the purposes of this study we assumed that species composition, when summed over the water column, was constant along the transect, that distributions of body condition and orientation remained constant and that the variability in integrated volume

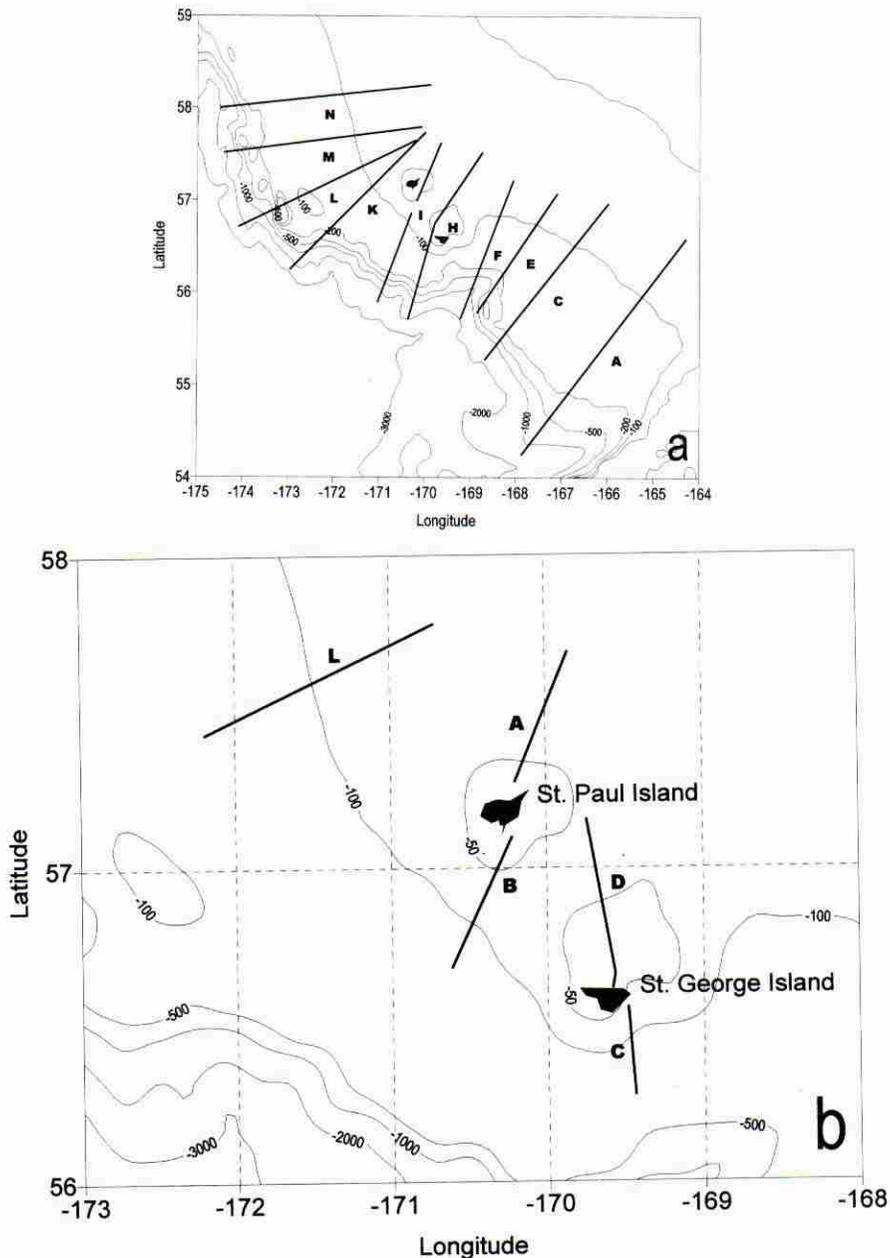


Fig. 1. Transects surveyed during a) 2–22 September 1994, and b) 10–25 September 1995. Depth contours in meters.

backscattering (in units $\text{m}^2 \text{n.mile}^{-2}$), a.k.a. acoustic return, reflected changes in the number of individuals per unit area of sea surface or prey biomass density (Hewitt and Demer 1993).

Data on thick-billed murres feeding or sitting on the water were selected from data on all behaviors for the present analysis. It is commonly assumed that seabirds sitting on the water are likely to feed or have recently fed in the immediate area (Hunt et al. 1988, Hunt and Harrison 1990, Hunt et al. 1990, Decker and Hunt 1996).

Because spectral analysis is sensitive to zero-counts in transect data (Fasham 1978, Star and Cullen 1981), only transects where murres were relatively numerous were used for further analysis. A minimum of 50 murres per transect was arbitrarily chosen as the cut-off for inclusion in the spectral analysis. Zero-counts were not present in the acoustic data. In order to estimate the bivariate spectra for murres and integrated acoustic return, the density of murres (no. km^{-2}) over 370 m transect intervals was calculated from the continuous data.

Uni- and bivariate spectral analyses were conducted following procedures described in Jenkins and Watts (1968), Platt and Denman (1975), and Chatfield (1984). The analyses were carried out in the time series analysis module of Statistica, release 5.1 (StatSoft 1996), which employs the Fast Fourier Transformation algorithm. Murre and integrated acoustic return data were first log-transformed to linearize the relationship between the two series along each transect. The murre and acoustic series were then aligned so that maximum cross-correlation occurred at zero lag, a procedure that has been shown to reduce the bias in both the phase and coherency estimators (Jenkins and Watts 1968). The overall mean of each series was subtracted prior to analysis to minimize spurious peaks at a frequency of zero. Finally, linear trends in the transformed data series were removed. The spectra were smoothed using a Tukey smoothing window (Platt and Denman 1975) with a width of $N/20$, where N is the number of 370 m segments along each transect. This smoothing window was chosen as a balance between resolution and accuracy. Log-log plots of spectral density versus measurement scale (a.k.a. power spectra) were then produced, the area under the curve in these plots is proportional to the variance. Phase spectra, which shows the degrees of offset between the series as a function of scale; and coherency spectra, which shows squared coherency as a function of scale, were also produced.

Averaged spectra were created by calculating the mean spectral density, phase and squared coherency at each measurement scale across all nine transects. Spectral density values were standardized by the variance of each series before calculating the means (Weber et al. 1986).

The slopes of the power spectra were estimated by linear regression. If the residuals were not randomly distributed with respect to predicted values, then the data were divided into two subsets and slopes were estimated for each section separately. Potential locations of data divisions ("breakpoints") were based on a combination of piecewise regression (StatSoft 1996) and visual estimation. Separate regressions were estimated with data above and below each potential breakpoint. The breakpoint that provided the best fit of the data to the separate regressions (greatest R^2 values) and random distributions of residuals was selected for further comparisons.

Results

The average power spectra for thick-billed murres and integrated acoustic return, representing the longer temporal scale of months, were similar in shape. No dominant peak in spectral density was evident and the slopes were shallow at small measurement scales and steep at larger scales (Fig. 2). The distribution of residuals

indicated that a single linear regression was not appropriate for either the murre or acoustic average spectra. However, separate linear regressions of subsets of the data resulted in more uniformly distributed residuals for both spectra. The breakpoints between the shallow and steeply sloping portions of the spectra indicated by the fit of the separate regressions were 2.7 km for the murre spectrum and 1.6 km for the acoustic spectrum (Fig. 2). For both spectra the regressions below the breakpoint did not explain a significant portion of the variation and the slopes were similarly not significant (murres: $R^2 = 0.009$, $p = 0.86$, $\beta = -0.02$, $n = 111$; acoustic return: $R^2 = 0.007$, $p = 0.20$, $\beta = -0.14$, $n = 84$). However, the regressions for the spectra above the breakpoint explained a significant amount of the variation and the slopes were significant and steep (murres: $R^2 = 0.84$, $p < 0.001$, $\beta = 0.92$, $n = 41$; acoustic return: $R^2 = 0.89$, $p < 0.001$, $\beta = 0.94$, $n = 68$).

The average bivariate spectra for the relationship between murres and integrated acoustic return indicated that the two spectra were in phase at almost all measurement scales and that coherency was non-zero at all scales, the lowest value for squared coherency was 0.05 (Fig. 3).

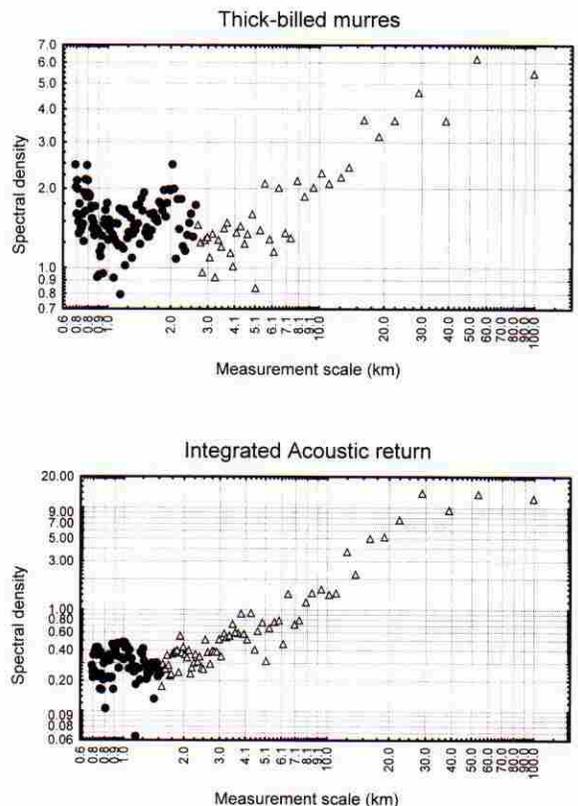


Fig. 2. Average power spectra from univariate spectral analysis of thick-billed murres and integrated acoustic return. Solid circles represent data below the breakpoint for separate regressions on subsets of the data. Open triangles represent data above the breakpoint.

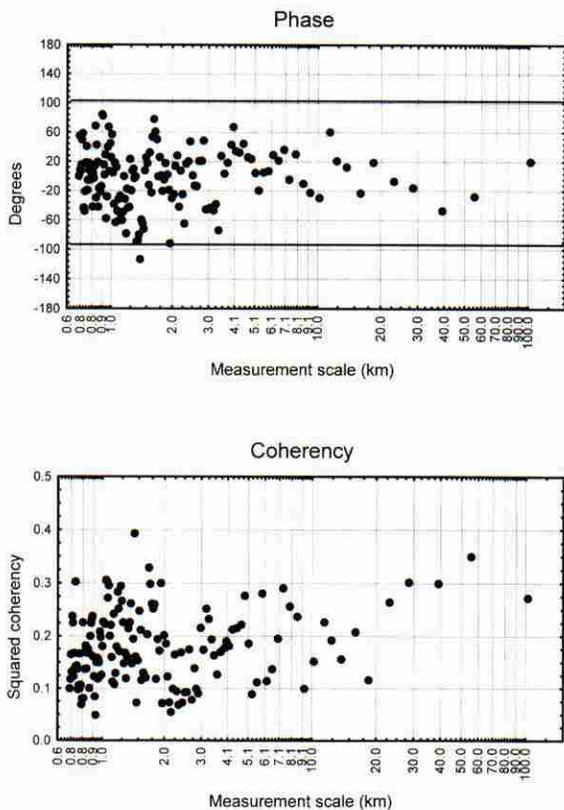


Fig. 3. Average phase and coherency spectra from bivariate spectral analysis of thick-billed murres and integrated acoustic return. A line is drawn at $+90^\circ$ and -90° on the phase spectrum.

None of the acoustic power spectra from individual transects had a dominant peak in spectral density. Five of the nine acoustic power spectra showed a similar pattern as the average acoustic spectrum – a shallow or negative slope at small measurement scales and a relatively steep positive slope at larger scales (Fig. 4). As was true for the average acoustic spectra, residuals from single regressions were not acceptable, whereas separate regressions for data below and above a breakpoint in measurement scale resulted in an improvement in the distribution of residuals. For all five acoustic transects, the slopes above the breakpoints were significant, positive and greater than the slopes below the breakpoints. Breakpoints ranged from measurement scales of 1.4 km to 3.0 km with an average of 2.4 km (Table 1). To simplify discussion, these five acoustic spectra will be referred to as “type A” for the remainder of this paper. The remaining four acoustic spectra were described well by a single regression equation (Table 2 and Fig. 5). These spectra will be referred to as “type B”.

Four of the five thick-billed murre spectra from transects with type A acoustic spectra had the pattern of zero or negative slopes at small measurement scales and positive slopes at large scales (A94, F, L-B, N)

(Table 1 and Fig. 4). The spectra for the fifth transect (M) had a positive slope at small scales and zero slope at large scales. All five spectra were best described by separate linear regressions of subsets of the data. Breakpoints between subsets ranged from measurement scales of 2.2 km to 4.1 km for an average of 3.4 km (Table 1 and Fig. 4).

Two of the four thick-billed murre spectra from transects with type B acoustic spectra fit a linear regression with a positive slope (transects A95 and L-A) (Table 2 and Fig. 5). The murre spectrum from transect C95 was also linear, but the slope was negative. The murre spectrum from transect L-C did not fit a single linear regression.

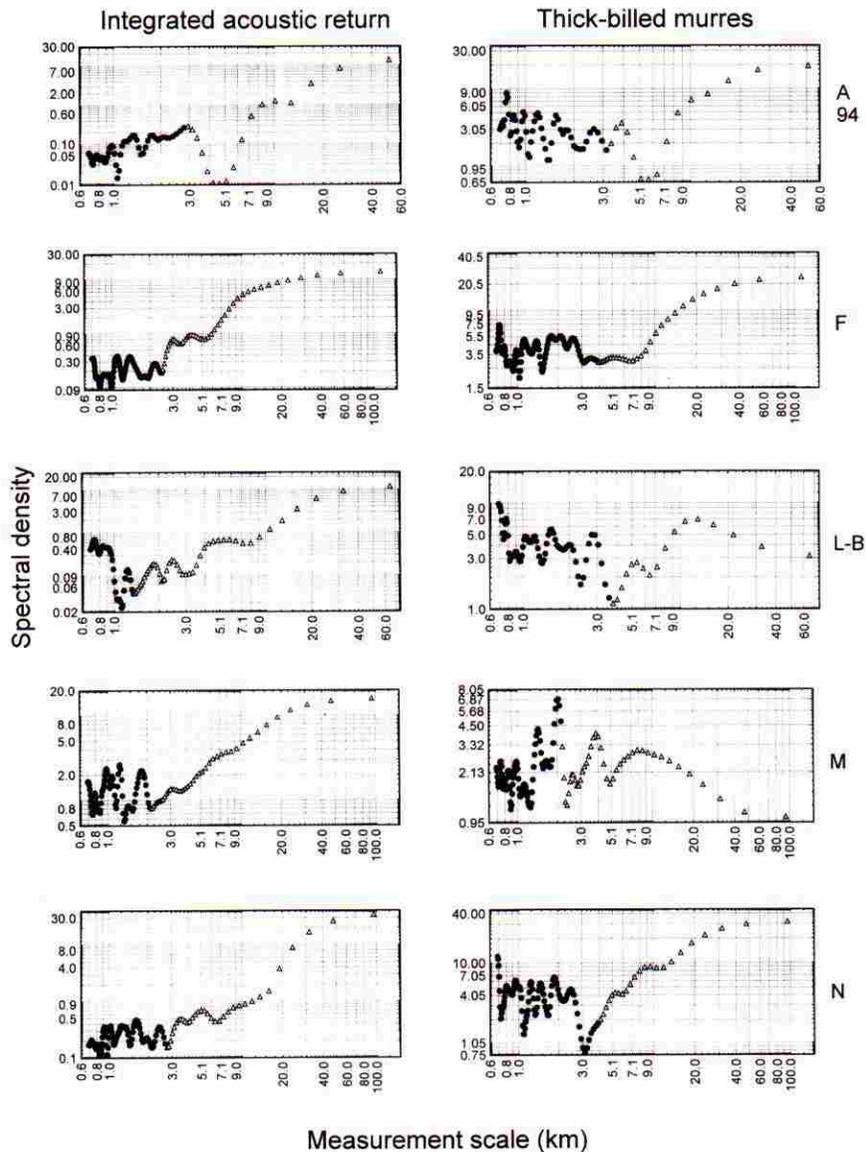
The bivariate spectra for type A acoustic transects show that at large measurement scales thick-billed murres and integrated acoustic return were consistently in phase and phase was a relatively smooth function of scale (Fig. 6). At smaller scales the relationship between scale and phase became erratic, the degrees of offset between the series fluctuated with scale instead of remaining relatively constant. Shifts out of and back into phase were also indicated (Fig. 6). The measurement scale at which the phase spectra became erratic ranged from 3.7 km to 5.6 km for an average of 4.9 km (Table 1 and Fig. 6). Coherency for these bivariate spectra was generally high at large spatial scales, decreased to nearly zero as scale decreased and then fluctuated between high and low values with further decreases in scale (Fig. 6). A threshold squared coherency of 0.02 was arbitrarily selected to indicate a value “near zero”. The measurement scale at which squared coherency first dropped to a value <0.02 from higher values at larger scales ranged from 2.8 to 12.5 km for an average of 4.3 km (Table 1 and Fig. 6).

Two of the four bivariate spectra for type B acoustic transects show that thick-billed murres and integrated acoustic return were in phase at large scales (transects A95 and L-C) (Fig. 7). The spectra for the other two transects, C95 and L-A, were out of phase at large scales (Fig. 7). All four spectra show that the relationship between scale and phase became erratic at smaller scales, ranging from 3.3 km to 10 km for an average of 5.1 km (Table 2 and Fig. 7). The measurement scale at which squared coherency first dropped to a value <0.02 from higher values at larger scales ranged from 1 km to 11 km for an average of 5.3 km (Table 2 and Fig. 7).

Discussion

We used spectral analysis to conduct a multiscale investigation of thick-billed murres and acoustic estimates of prey biomass in the southeastern Bering Sea. Spectral analysis has been successfully applied to the study of plankton distributions (Platt et al. 1970, Denman and

Fig. 4. Power spectra for integrated acoustic return and thick-billed murres along transects with type A acoustic spectra (transects A94, F, L-B, M, and N). Solid circles represent data below the breakpoint for separate regressions on subsets of the data. Open triangles represent data above the breakpoint.



Platt 1974, Powell et al. 1975, Fasham and Pugh 1976, Richerson et al. 1978, Mackas and Boyd 1979, Weber et al. 1986); however, fewer studies have used this procedure to investigate spatial variance patterns and correlations between prey and more mobile aquatic predators such as fish (Rose and Leggett 1990, Horne and Schneider 1994) and seabirds (Schneider 1989). Similar to previous studies (Schneider 1989, Rose and Leggett 1990), we found that spatial variance and coherence of predators and prey depended on spatial scale. Our results suggest, further, that the scale-dependent changes in coherence were related to changes in spatial variance of prey. In addition, we observed several patterns in the spectra for individual transects, representing a temporal scale of hours, that were not

apparent in the survey-wide average spectra, representing a temporal scale of months.

The average power spectra for thick-billed murre density and integrated acoustic return (an estimate of prey biomass) were similar in shape. Both were characterized by zero slope over a range of small spatial scales, changing to a positive slope at larger scales. The formation of aggregations is one mechanism that can produce changes in the slope of spectral density versus scale (Horne and Schneider 1997). Thus one interpretation of the average spectra is that murres were forming aggregations at spatial scales of ca 3 km and greater, and prey were forming aggregations at scales of ca 2 km and greater. Because the area under the curve in a log-log plot of spectral density versus measurement

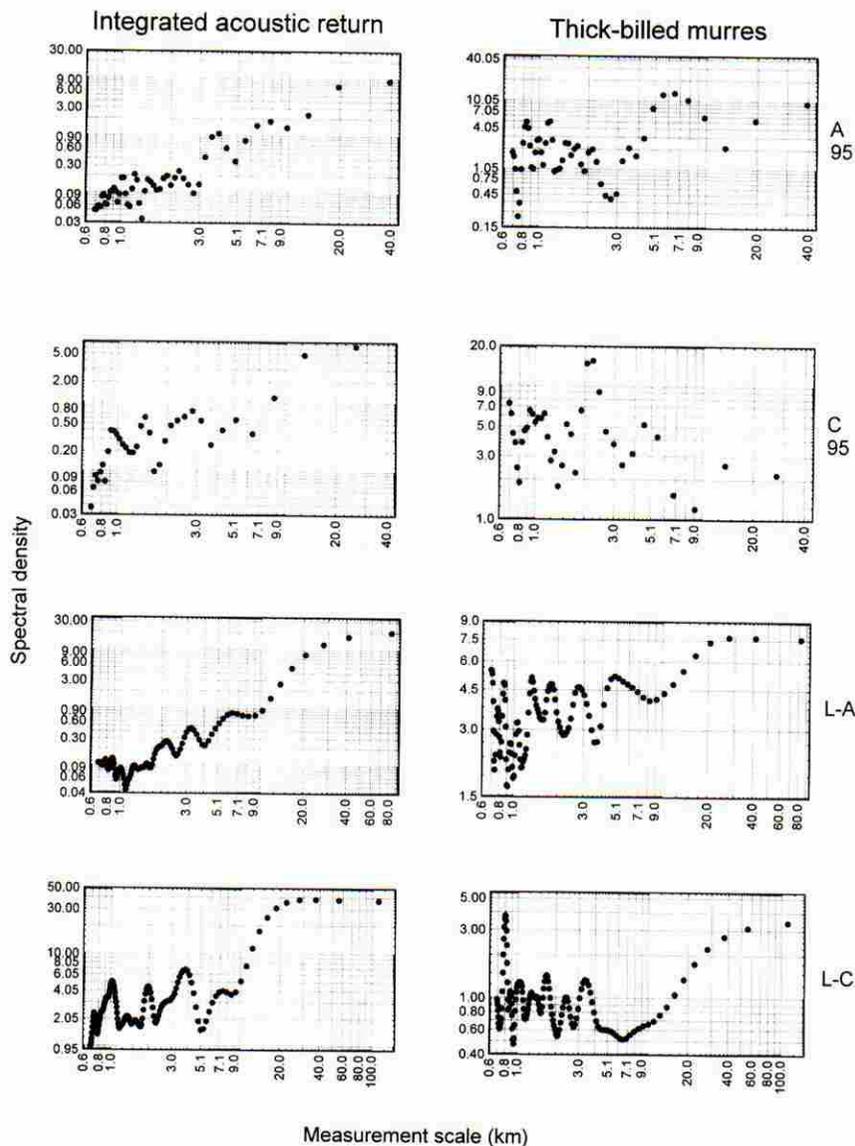


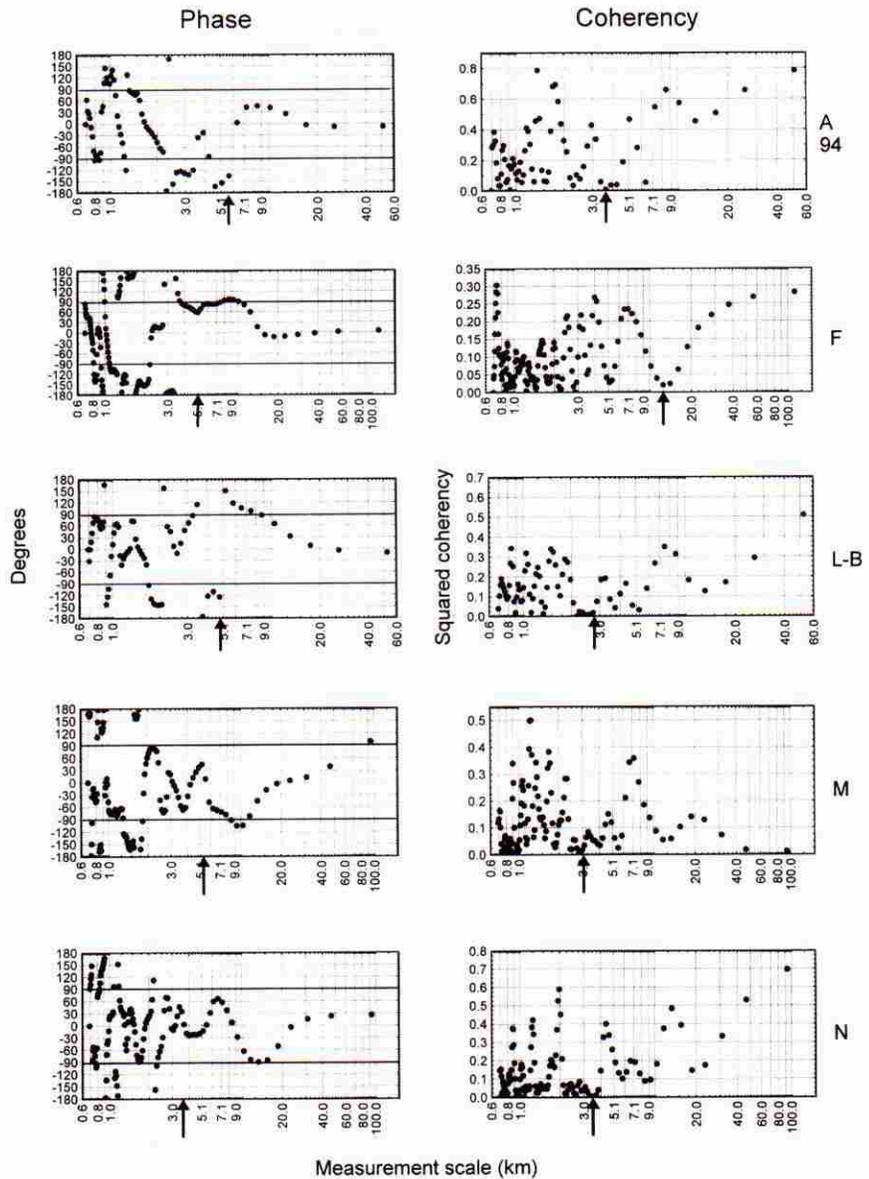
Fig. 5. Power spectra for integrated acoustic return and thick-billed murres along transects with type B acoustic spectra (transects A95, C95, L-A, and L-C).

scale is proportional to spatial variance, the average spectra also indicate that at the smallest scales spatial variance of murres and prey was relatively low.

The average power spectra for murres differs from the pattern observed for krill, a mobile marine crustacean abundant in the southern Ocean. Weber et al. (1986) found that the slopes of spectral density plots for krill distributions were near zero over the range of scales studied (1–100 km). The authors interpret the shallow slope of the krill spectra as indicating the formation of aggregations at the smallest scales (km), reasoning that this would result in an increase in spatial variance at small scales and a decrease in the slope of the power spectra. Weber et al. (1986) suggest that krill aggregations form as a result of behavior on the part of the krill. Our data indicate that murres formed

aggregations at larger scales than did krill (km to tens of km). This difference in the scale of aggregation could be a result of murres forming flocks of greater extent and spacing than krill swarms, possibly due to the much greater body size of murres compared to krill (Wiens 1989). The scale of murre aggregation may also result from the aggregation patterns of their prey. In addition to similarities between the power spectra of thick-billed murres and acoustic estimates of prey biomass, we found that the average bivariate spectra were in phase and had a non-zero coherence at nearly all scales. This result indicates a positive correlation between murres and prey at all scales and thus provides support for the hypothesis that the distribution of murres was influenced by the distribution of their prey.

Fig. 6. Phase and coherency spectra for integrated acoustic return and thick-billed murres along transects with type A acoustic spectra (transects A94, F, L-B, M, and N). A line is drawn at $+90^\circ$ and -90° on the phase spectrum. Arrows mark measurement scale at which phase becomes erratic or coherency drops to <0.02 .



In contrast to the average spectra, the bivariate analysis of individual "type A" transects showed that the murre and prey spectra were consistently in phase only at relatively large spatial scales. Furthermore, phase fluctuated erratically with scale at scales below ca 5 km. It has been shown, theoretically, that where phase is a smooth function of measurement scale, squared coherency is usually significantly different from zero, but where phase oscillates rapidly with scale, squared coherency is usually low and not significant (Platt and Denman 1975). Since the bias in the phase estimator is generally small whereas the bias in the coherency estimators can be large even after alignment (Jenkins and Watts 1968), the appearance of the phase spectrum may be a better indicator of correlation than the coherency

spectrum. The phase spectra thus suggest that the correlation between murres and prey along "type A" transects was positive and significant at larger scales but dropped to a value that was likely insignificant at scales below ca 5 km.

Scale-dependent correlations between consumers and resources have been documented in other systems, marine and terrestrial, primarily using more traditional correlation statistics (Rotenberry and Wiens 1980, Wiens and Rotenberry 1981, Schneider and Piatt 1986, Wiens et al. 1986, Morris 1987, Heinemann et al. 1989, Piatt 1990, Hunt et al. 1990, 1992, Hunt 1991, Brown and Morgan 1995). It has been suggested that poor small-scale correlations may be a result of predators not being able to track prey at relatively small spatial

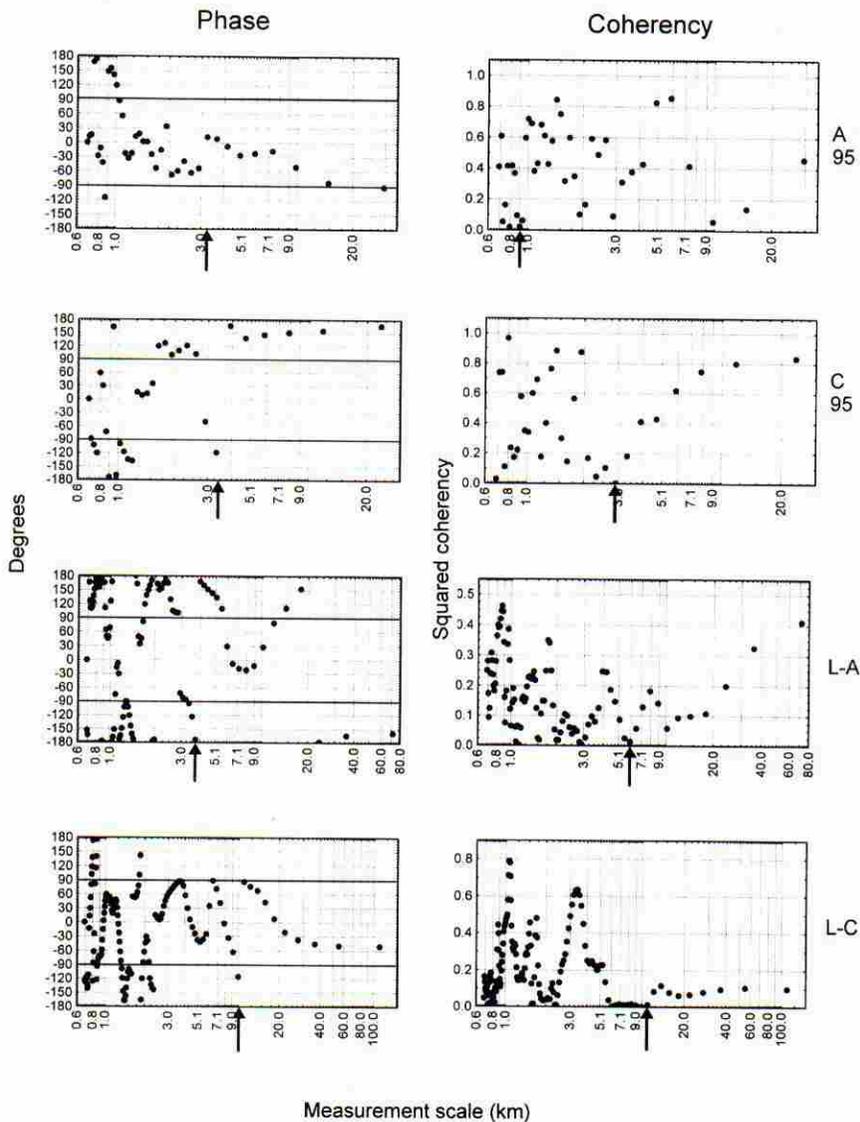


Fig. 7. Phase and coherency spectra for integrated acoustic return and thick-billed murres along transects with type B acoustic spectra (transects A95, C95, L-A, and L-C). A line is drawn at $+90^\circ$ and -90° on the phase spectrum. Arrows mark measurement scale at which phase becomes erratic or coherency drops to < 0.02 .

scales (Schneider and Piatt 1986, Heinemann et al. 1989, Hunt et al. 1990, Hunt 1991), or prey avoidance behavior (Schneider and Piatt 1986, Logerwell and Hargreaves 1996). However, knowledge of the spatial variance structure of prey/resources may put these kinds of results in a different context. The pattern indicated by the type A prey spectra indicates: 1) a range of small scales, < 2.4 km on average, over which prey spatial variance was relatively low and unchanging and 2) a range of larger scales (> 2.4 km) over which prey spatial variance increased rapidly. As discussed above, the phase spectra suggest that the correlation between murres and prey decreased to near zero at a scale ca 5 km. These two patterns, considered together, indicate that the correlation between murres and prey was poor at spatial scales where prey distribution was relatively uniform. This leads to an alternative to the hypotheses

that predators do not track prey well at small spatial scales or that prey avoidance behavior results in poor small-scale correlations. Consumers and resources may instead be poorly correlated at small scales because resource distribution is relatively uniform. This leads to an alternative to the hypotheses that predators do not track prey well at small spatial scales or that prey avoidance behavior results in poor small-scale correlations. Consumers and resources may instead be poorly correlated at small scales because resource distribution is relatively uniform at small scales resulting in only a minor increase in foraging return for organisms showing an aggregative response to variations in resource density at these, smaller scales. Mathematical modeling of foraging intake relative to prey and predator spatial pattern would be one way to examine this hypothesis; however, this is beyond the scope of the present paper.

Table 1. Summary statistics for power and bivariate spectra of thick-billed murres and integrated acoustic return from transects with type A acoustic spectra. "Breakpoints" are the measurement scales that represent data divisions for separate linear regressions (see Methods). R^2 and β values from linear regressions on subsets of data below and above the breakpoints are statistically significant at the $p < 0.05$ level. "NS" indicates a non-significant R^2 or β value. For bivariate spectra, the measurement scales at which the phase becomes erratic with decreasing scale, and at which squared coherency drops to < 0.02 are reported.

Transect	Univariate spectra										Bivariate spectra	
	Acoustic return					Thick-billed murres					Phase erratic	Coherency near 0
	break-point	R^2 below	β below	R^2 above	β above	break-point	R^2 below	β below	R^2 above	β above		
A94	3.0 km	0.58 n = 52	0.77	0.62 n = 18	0.80	3.2 km	0.18 n = 53	-0.42	0.58 n = 17	0.78	5.6 km	3.6 km
F	2.5	NS n = 108	NS	0.87 n = 45	0.94	4.0	NS n = 125	NS	0.89 n = 28	0.95	5.1	12.5
L-B	1.4	0.61 n = 41	-0.79	0.91 n = 47	0.96	3.7	0.61 n = 71	-0.79	0.32 n = 18	0.60	4.7	2.8
M	2.2	NS n = 84	NS	0.96 n = 44	0.98	2.2	0.34 n = 85	0.59	NS n = 43	NS	5.2	3.0
N	2.8	0.11 n = 96	0.34	0.89 n = 33	0.95	4.1	0.21 n = 106	-0.45	0.91 n = 23	0.96	3.7	3.6
Mean	2.4 km					3.4 km					4.9 km	4.3 km

The use of spectral analysis to investigate predator-prey spatial patterns has some limitations. For instance, spectral analysis is not appropriate for data series that are not periodic but instead have a single, broad coherent feature such as one large aggregation of individuals (Armi and Flament 1985). Transect data for both murres and prey (integrated acoustic return) showed few cases where single aggregations dominated; nonetheless, this sort of error could have resulted in underestimates of spatial variance. Because the slopes of spectral density plots have been shown to decrease as the mean count per sample decreases (Fasham 1978), the presence of zeros in the transect data is another potential source of error. We attempted to minimize this source of error by selecting transects with relatively high numbers of murres, but we were not able to entirely avoid zero counts in the murre data. Sources of error in the

bivariate spectral analysis include random sampling error of a Poisson process, which can lower coherence values (Mackas 1977).

In summary, the average uni- and bivariate spectra for thick-billed murre density and acoustic estimates of prey biomass in the southeastern Bering Sea indicated that murres and their prey had similar spatial variance patterns and were positively correlated over the range of spatial scales studied. The average spectra, calculated from transect data collected over the duration of a two-year study, can be interpreted as representing patterns occurring over temporal scales on the order of months. Spectra from individual transects, on the other hand, represent temporal scales on the order of hours, and showed several patterns that were not evident in the average spectra. In particular, the individual spectra showed that the correlation between murres and prey

Table 2. Summary statistics for power and bivariate spectra of thick-billed murres and integrated acoustic return from transects with type B acoustic spectra. R^2 and β values from linear regressions are statistically significant at the $p < 0.05$ level. "NS" indicates a non-significant R^2 or β value. For bivariate spectra, the measurement scales at which the phase becomes erratic with decreasing scale, and at which squared coherency drops to < 0.02 are reported.

Transect	Univariate spectra				Bivariate spectra	
	Acoustic return		Thick-billed murres		Phase erratic	Coherency near 0
	R^2	β	R^2	β		
A95	0.87	0.93	0.19	0.46	3.3 km	1.0 km
C95	0.67	0.83	0.10	-0.35	3.4	3.0
L-A	0.87	0.93	0.36	0.60	3.8	6.0
L-C	0.57	0.76	NS	NS	10.0	11.0
MEAN					5.1 km	5.3 km

was scale-dependent, being relatively strong at large spatial scales, but decreasing at smaller scales. Our observation that the correlation between murre and prey was poor at scales where prey variance was relatively low suggests a new hypothesis regarding foraging energetics at multiple scales that may explain the poor small-scale correlations between consumers and resources that have been observed in a number of other systems. Finally, the differences we observed in patterns among spatial scales and between the averaged and individual data series illustrate the ways in which ecological patterns can vary with temporal as well as spatial scale.

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