

from: "Patch Dynamics" , Levin, Steele and Powell, eds
1992

pp 7-39

1493

6

DESCRIPTION AND ANALYSIS OF SPATIAL PATTERNS

Graciela García-Moliner, Doran M. Mason, Charles H. Greene, Agustín Lobo, Bai-lian Li, Jianguo Wu, and G. A. Bradshaw

INTRODUCTION

Spatial pattern is a conspicuous characteristic of any ecosystem and has received much attention from researchers over the last decade and a half (e.g., Steele 1978, Pickett and White 1985, Kolasa and Pickett 1991), most recently under the name of landscape ecology (Forman and Godron 1986, Turner and Gardner 1991). Description of patchiness in marine, freshwater, and terrestrial systems presents different problems, particularly in terms of mechanisms of patch formation (e.g., Wiens 1976 and Pickett and White 1985 in terrestrial systems; and Legendre and Demers 1984, Mackas et al. 1985, Hamner 1988, Barry and Dayton 1991, and Downing 1991 in aquatic systems). Deutschman et al. (this volume) supply specific examples of mechanisms of patch formation.

In this chapter we attempt to describe patchiness in ecosystems and a set of analytical tools useful for the study of spatial pattern across different scales and systems. Specifically, we address three topics: (1) the description of patches in relation to scale, (2) sampling a patchy environment, and (3) the analysis and interpretation of spatial data. Additionally, marine and terrestrial ecosystems will be contrasted and compared to elucidate the inherent differences between the two very different systems.

PATCHES AND PATCHINESS

Description of a "Patch:" The Terrestrial Concept

When the distribution of a phenomenon on land becomes discontinuous, the system is considered to be "patchy." A patch at the landscape scale may contain a certain number of within-community patches consisting of aggregates of physical entities and biological individuals, which in turn may exhibit patchiness on finer scales—a "hierarchical scheme" (Wiens 1976). At the community level, a patch may consist of a tree gap or a gopher mound. Although all patches are realistically three-dimensional, humans generally perceive patches in lower dimensionality. The term *patch* typically tends to emphasize spatial discontinuity and internal homogeneity, but patches may vary greatly in geometry, content, heterogeneity, and boundary characteristics.

Patchiness: The Marine Concept

The terrestrial phenomenon of a discontinuous patch has dominated the landscape literature. However, ecological processes in the ocean associated with spatio-temporal scales of water movement reveal "patchiness" rather than patches. These are dealt with through the Stommel diagrams (Haury et al. 1978) revised by Marquet et al. (this volume). The inherent fluid-dynamic nature of the environment necessitates a different set of criteria (Legendre and Demers 1984). Patches in the sea are best defined by the purpose of the study, the processes that create the patch, and the scale of the sampling. This is an indication of basic differences in the terrestrial and marine systems; or between substrate-dependent (intertidal and benthic) and substrate-independent (pelagic) systems. From this perspective, the intertidal and benthic marine ecosystems are viewed in a similar manner to terrestrial systems, defined in terms of the absence of an entity or open space where the boundaries are often discrete. Intertidal zones where high-energy wave activity removes assemblages of organisms and leaves behind a barren patch open for colonization (Paine and Levin 1981) are similar to gaps in forest stands.

Pelagic organisms and plants are often aggregated through physical, chemical, and behavioral processes. Physical phenomena such as fronts and Langmuir circulation can produce linear concentrations of planktonic organisms (e.g., Denman and Powell 1984, Mackas et al. 1985).

SAMPLING

One of the main problems in describing patchiness is the large rate of spatial change in the ocean, compared to terrestrial systems. As a result, there have to be major differences in the sampling design. The physical factors include: three-dimensional motion; absence of physical barriers to vertical and horizontal migration (Hamner 1988); low requirement of structural support for biota due to high specific gravity of water (Parsons 1976); and damping of short-term thermal variability due to high specific heat content of water (Steele 1985). Differences between the two systems' biology include: dominance of poikilotherms at the higher trophic levels; life history strategies (Steele 1985); and the small size of primary producers vs. the large size of primary producers of terrestrial ecosystems (Issacs 1977). It is these differences that present distinct sampling challenges in marine and terrestrial ecosystems.

The results of these differences are evident in the data obtained and, in consequence, in the methods used in analysis. Thus, it is relatively easy to run long transects on a ship sampling continuously for certain physical and biological parameters. This allows the use of data-intensive analytical methods such as Fourier analysis. On the other hand, there are problems in the temporal resolution of these time series: Are they truly synoptic?

On land it is usually extremely difficult to get long transects, and so methods such as geostatistics have been developed (see van Es, this volume). However, the problems in reconciling spatial and temporal variability are very much less on land.

In both sectors, satellite imagery can provide an entirely new, and different, view of each environment. Thus, in the ocean, color data has provided details of the two-dimensional fine structure and has radically altered our perceptions of smaller scale structure. On land, the opposite is true, and remote sensing has opened up the potential for large-scale analysis and modeling.

ANALYSIS TECHNIQUE, DATA SETS, AND EXAMPLES

Conventional statistical techniques, such as ANOVA, are not well suited for use on spatial data sets due to the assumptions of independence and normality. In spatially derived data sets, observations are generally not independent but rather are spatially correlated at some scale of resolution. Thus, other techniques must be used when analyzing spatial data sets. The analytical techniques for the study of spatial patterns or the variability in patchiness treated in this chapter include autocorrelation function (ACF), power spectra, wavelets, multivariate analysis, empirical orthogonal functions (EOF), and fractals.

A general review on description and analysis of the determination of spatial pattern on land can be found, for example, in Legendre and Fortin (1989) and references therein (see also van Es, this volume). In the oceans, power spectral analysis is probably the most widely used technique for pattern recognition with transect data (e.g., Platt and Denman 1975, Barale and Trees 1987, Barale 1987). Deutschman et al. (this volume) have analyzed krill data using both spectral analysis and wavelet transforms (see also the section on wavelet analysis later in this chapter) and in addition have developed a model (discussed in Grünbaum 1991) to describe the interactions between physical phenomena and behavioral interactions in Antarctic krill. Overall, the coupling of biotic/abiotic phenomena is a major factor in determining pattern and in differentiating pattern and process (Abbott, Denman, this volume).

Analyses of Time-Series and Spatial Series Data: The Autocorrelation Function and the Spectral Density Function

The autocorrelation function (ACF) and the spectral density function (power spectrum) are two of the most widely used diagnostic tools in signal processing (Jassby and Powell 1990). The power spectrum is the Fourier transform of the autocovariance function. The power spectrum decomposes the total variance in the data set into component contributions associated with each wave number in the spatial range of interest. The estimated spectrum may exhibit peaks at those wave numbers that contribute most to oscillations of the recorded variable in space.

For shorter series, analysis of the ACF often provides more reliable results (Jassby and Powell 1990). The ACF is used to quantify autocorrelations among points in a time series or one-dimensional spatial series separated by different temporal or spatial lags.

These techniques are useful only for analyzing one-dimensional serial data (Chatfield 1984). For two-dimensional data sets there are two-dimensional Fourier methods and geostatistics, but these essentially convert the data to one spatial scalar. The problem of pattern recognition, which the human eye does so easily, is still analytically intractable (e.g., Mandelbrot 1983).

Examples from biological oceanography. Spectral analysis has a relatively long history of use in physical oceanography, a field in which periodic phenomena are commonly encountered (e.g., Stommel 1963). The method was introduced to biological oceanography in the mid-1970s (Platt and Denman 1975) and has yielded a variety of interesting results for theoretical ecologists to ponder (e.g., Steele 1985, Powell 1989).

Recently, Levin (1990) compared the spectra for Antarctic krill, temperature, and chlorophyll data from the Southern Ocean (Figure 1). Temperature and chlorophyll spectra were similar at all scales, but the krill spectrum was flatter at higher wave numbers (smaller

spatial scales: less than 20 km).⁷ Levin hypothesized that this finding might be indicative of physical processes driving the large-scale distributions of all three variables and of biological processes, specifically active aggregation behavior, driving the krill distributional patterns at smaller spatial scales.

With Levin's hypothesis in mind, we set out to analyze the fine-scale (meters to 10s of meters) patterns of krill in a data set collected by Greene et al. (in press) from three different sound-scattering layers (SSLs) in the Gulf of Maine (Figure 2). The species of krill (*Meganyctiphanes norvegica*) studied in the Greene et al. investigation was different from the species (*Euphausia superba*) discussed by Levin (1990) and by Deutschman et al. (this volume). Although *Meganyctiphanes norvegica* is rarely found to school or actively aggregate as intensively as *Euphausia superba*, we had some evidence of patchiness in the observed fine-scale patterns (Table 1; Greene et al., in press). Therefore, we were interested in determining whether or not the ACF could improve our characterization of the observed fine-scale patchiness.

The results of the analyses did little to improve our characterization of the observed fine-scale patchiness. The ACF was found to drop off rapidly with increasing spatial lag in data from all three SSLs. In only four out of the 15 cases analyzed were the autocorrelations significant at one lag interval (Table 2), and in no cases were they significant at two or more lag intervals. These results suggest that the characteristic length scales of patches were less than 1.5 - 3.0 m, and thus unresolvable by our sampling methods. The power spectra from the three SSLs were found to be flat (Figure 3), indicating no obvious periodicities in the observed fine-scale patchiness.

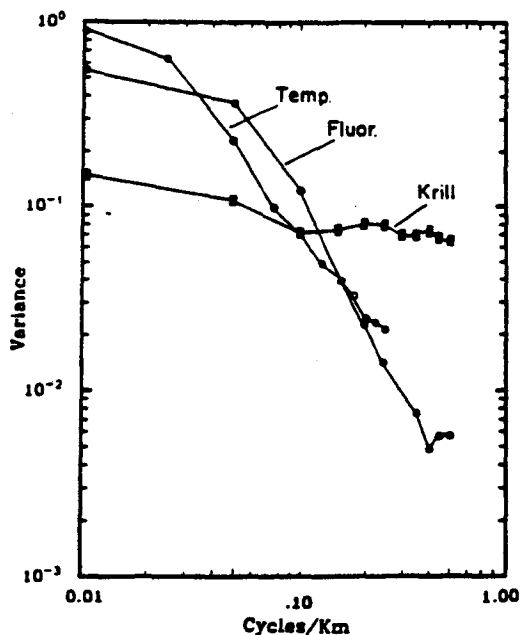


Figure 1. Mean spectral plots for Antarctic krill, chlorophyll fluorescence, and temperature from Levin (1990), as reprinted from Weber et al. (1986).

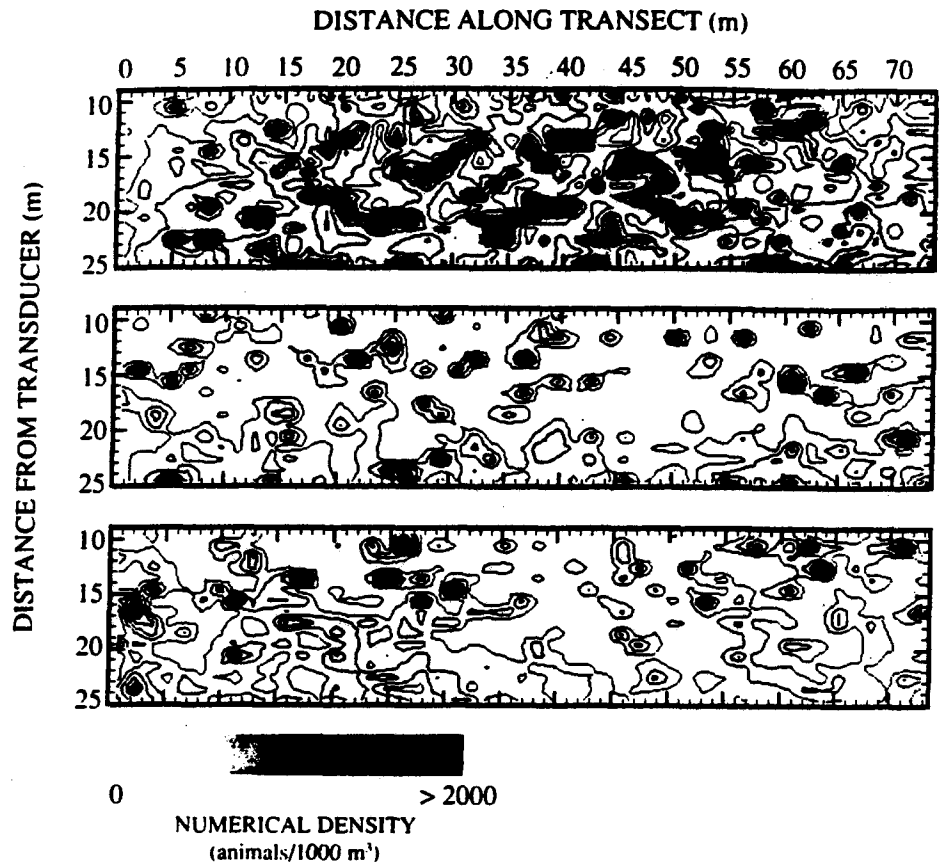


Figure 2. Fine-scale horizontal distributions of krill in a) daytime deep SSL (DDSSL), b) nighttime deep SSL (NDSSL), and c) nighttime shallow SSL (NSSSL). Numerical densities are given in units of animals per 1000 m³ (from Greene et al., in press).

Table 1. Numerical density and spatial aggregation statistics for krill in daytime deep SSL (DDSSL), nighttime deep SSL (NDSSL), and nighttime shallow SSL (NSSSL) from Gulf of Maine. Estimates of mean numerical density and Lloyd's (1967) index of mean crowding are given in units of animals per 1000 m³; Lloyd's index of patchiness is nondimensional.

	Mean Numerical Density (+2 SE)	Index of Mean Crowding	Index of Patchiness (+2 SE)
DDSSL	594 (26)	820	1.38 (0.04)
NDSSL	200 (18)	491	2.46 (0.24)
NSSSL	234 (18)	503	2.15 (0.16)

$$\text{Index of Mean Crowding} = \bar{x} = (s^2/\bar{x} - 1)(1 + s^2/n\bar{x}^2)$$

$$\text{Patchiness} = [\bar{x} + (s = s^2/\bar{x} - 1)(1 + s^2/n\bar{x}^2)]/x$$

where \bar{x} = mean, s^2 = variance,
 n = number of samples,
 and $1 + s^2/n\bar{x}^2$ is the sampling bias correction factor.

Comparisons of Mean Numerical Densities Among SSL's (ANOVA and Duncan's Multiple Range Test): DDSSL > NSSSL > NDSSL

Table 2. Autocorrelation at one spatial lag (1.5 m) for krill nighttime deep SSL (NDSSL), and nighttime shallow SSL (NSSSL) from Gulf of Maine. An asterisk indicates statistically significant autocorrelation; NS indicates nonsignificant autocorrelation.

	Transect Distance from Transducer (m)				
	21	22	23	24	25
	Autocorrelation				
DDSSL	0.227 NS	0.216 NS	0.247 NS	0.116 NS	0.419 *
NDSSL	0.096 NS	0.136 NS	0.410 *	0.391 *	0.119 NS
NSSSL	0.182 NS	0.250 NS	0.247 NS	0.160 NS	0.527 *

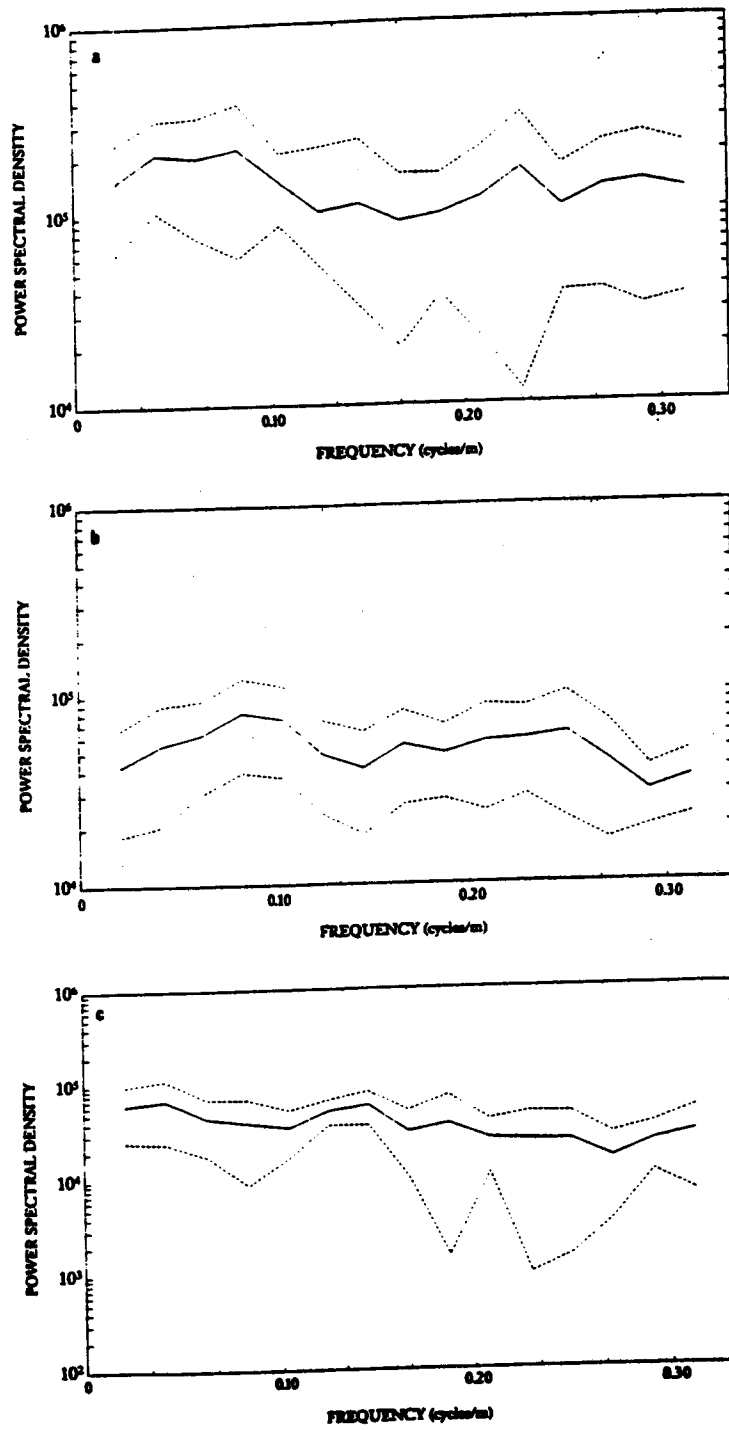


Figure 3. Power spectra for three SSLs: a) DDSSL, b) NDSSL, and c) NSSSL. Dashed lines correspond to 95% confidence intervals.

We infer from these results that, although *Meganyctiphanes* individuals exhibited significant fine-scale patchiness in the three SSLs examined (Table 1), the krill aggregations themselves tended to be relatively small and distributed more or less randomly in the environment. Greene et al. (in press) concluded that this type of fine-scale patchiness would be particularly difficult for predators to exploit in an efficient manner.

Wavelet Analysis

Wavelet analysis is a technique that has been employed for the analysis of spatial pattern and time series (Mallat 1988, Argoul et al. 1989, Bradshaw 1991). Three functions comprise wavelet analysis: the wavelet transform, wavelet variance, and the wavelet cross-covariance. The wavelet transform is defined in one dimension in the continuous form as:

$$\omega(a,x) = 1/a \int_{-\infty}^{\infty} f(x)g(x-b/a)dx \quad (1)$$

where $f(x)$ is the data function, $g(x)$ is the analyzing wavelet, a is the scale, and b is the point around which the wavelet is centered.

Similar to Fourier spectral analysis, the transform effects a scale-by-scale decomposition of the data. In contrast to spectral analysis, the transform is a local filter and, as a function of both scale, a , and position, x , it retains location information. Because of this property, the wavelet transform can be used to examine the relationship of spatial pattern across scales. This is particularly useful in cases where the data is hierarchical or multi-scalar in structure or the data is non-uniformly distributed along the transect (Bradshaw and Spies, in press). Thus, the presence and intensity of fine-scale features may be related to higher-order structures at coarser scales.

As an example of the method, the wavelet transform was calculated for a transect selected from a 1 m resolution digital image of a Douglas fir forest canopy in western Cascades, Oregon (Figure 4). The wavelet transform provides a graphical display of the hierarchical structure of the overall pattern: i.e., the pattern of the individual tree crowns at one scale nested in a higher-order pattern at which the individual trees are clustered (Figure 5).

The analyzing wavelet may be selected from several possible functions given certain admissibility requirements (e.g., Mexican hat and Haar wavelets, Daubechies 1988). For example, if one is interested in the detection of gradients or edges, a step function such as the Haar wavelet would be a suitable choice (Gamage 1990; see also next section). The Mexican hat function was used in the previous canopy example.

The wavelet variance is a function derived from the wavelet transform to facilitate the identification of dominant scale(s) (e.g., patch sizes) among two or more data sets. It is defined as

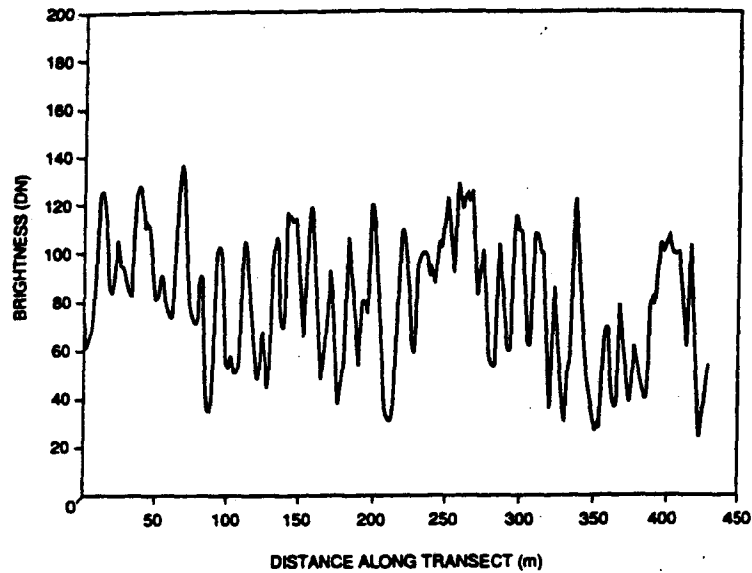


Figure 4. Transect of canopy brightness taken from a Douglas fir old growth stand using low-altitude videography (1 m resolution). The peaks and troughs in the data correspond to bright, illuminated tree crowns alternating with dark gaps in the canopy, respectively.

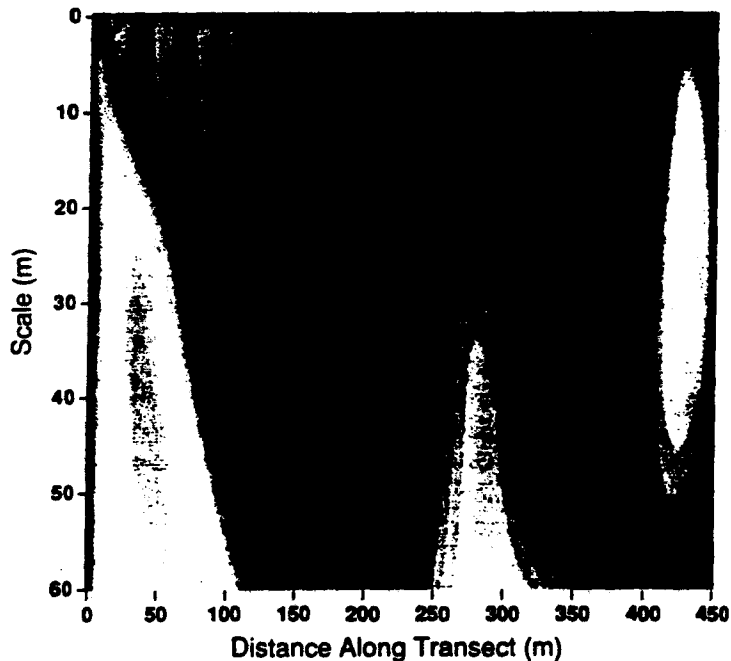


Figure 5. The wavelet transform calculated for the transect in Figure 4. The x-axis corresponds to location along the transect (meters). The y-axis indicates the scale of pattern. High (bright) values of the transform correspond to peaks, while low (dark) values correspond to troughs in the data. Note there are two dominant scales of pattern: a fine scale nested within the larger domains.

$$w(a) = \int_{-\infty}^{\infty} \omega^2(a, x) dx \quad (2)$$

The wavelet variance was calculated for the transect in Figure 5 and for four other transects taken from four forest canopies at distinct stages of development: young, mature, mature-old growth mixture, and a young-mature mixture. The peak and amplitude of the wavelet variance for each transect distinguish the canopy texture of each stand (Figure 6).

In terms of signal processing, the wavelet variance provides a measure of the average energy contributed by each scale (or frequency) to the overall signal. Although both Fourier power spectra and wavelet variances generally appear to provide similar information (Bradshaw 1991), in many cases the wavelet variance has the advantage of being used in concert with the hierarchical information provided by the wavelet transform.

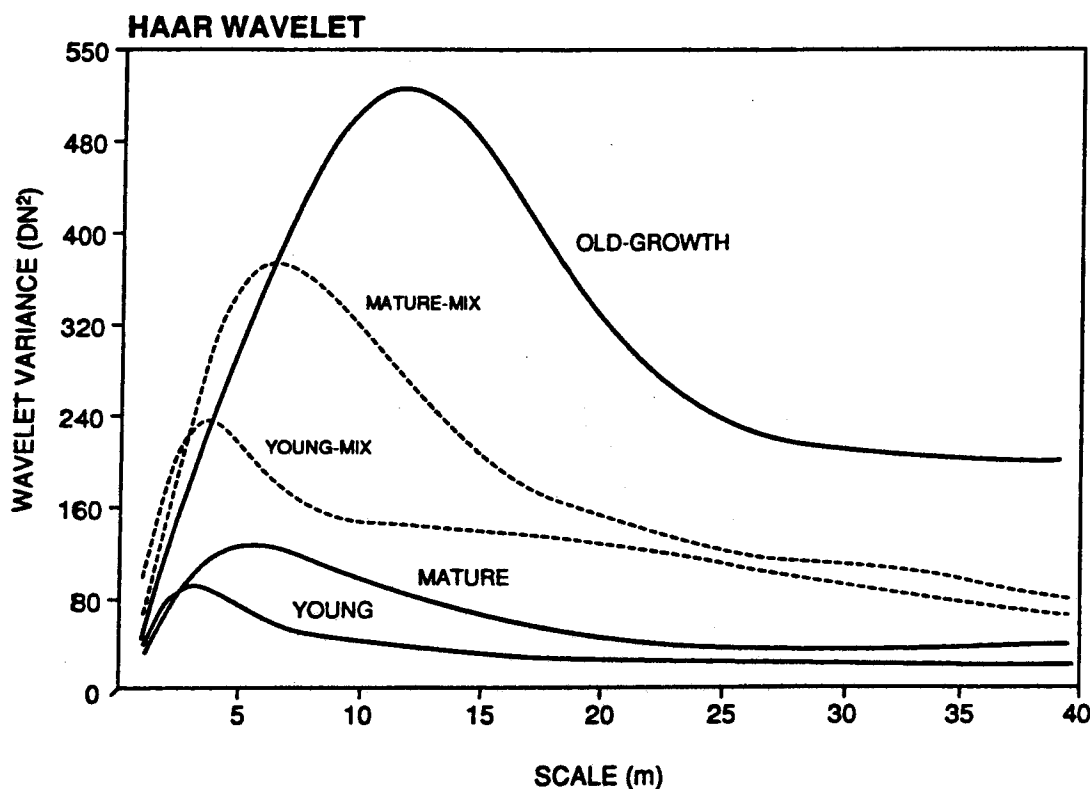


Figure 6. The wavelet variance calculated for canopy data as in Figure 4 for five forest age-class stands: young, mature, old growth, mature-old growth mixture, and young-mature mixture. The peak indicates the scale at which the pattern is dominated. The amplitude is proportional to the contrast in the data signal.

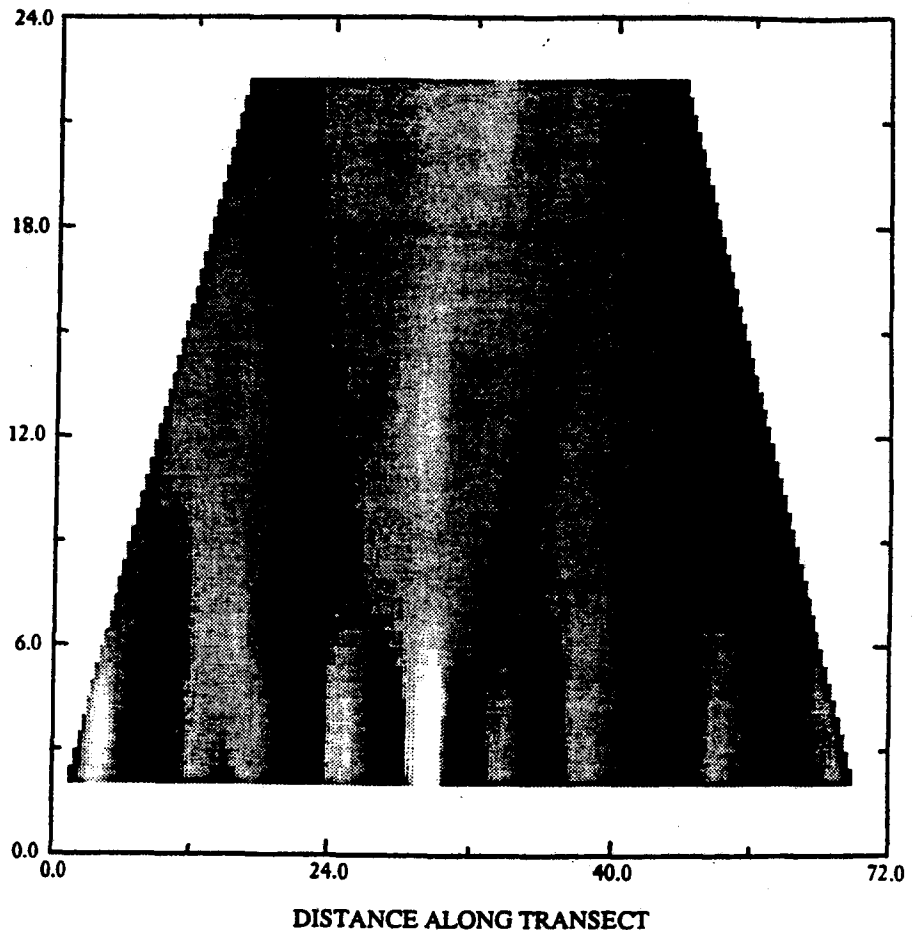


Figure 7. Wavelet transform showing changes in the intensity of the variance in krill abundance with scale and distance traveled along acoustic transect. The relative change in intensity occurred from white (high variance) to black (low variance).

The wavelet transform and the wavelet variance are performed using univariate data. A third function, the wavelet cross-covariance, was derived from the wavelet transform to quantify the spatial (or temporal) correlation between two variables as a function of scale and lag (Bradshaw 1991). The lag is defined as the absolute distance between two points. The wavelet cross-covariance function is obtained by first calculating the wavelet transform for each variable, followed by the calculation of the cross-covariance function of the transformed data at each scale. The scale(s) at which the maximum cross-covariance occurs indicates the patch size at which the two variables are correlated. The lag at which the maximum cross-covariance occurs provides a measure of how closely coupled the two variables are in space. For example, a maximum wavelet cross-covariance at 10 m zero lag between variables A and B indicates that the two variables are coupled in space in 10 m patches. Conversely,

a lack of correlation or a maximum cross-covariance at a non-zero lag at a given scale suggests that the two variables are poorly or less closely coupled. Thus, the wavelet cross-covariance function may be used to infer dominant scales of interaction. (An example is given in Deutschman et al., this volume).

Examples from Biological Oceanography. We reanalyzed the krill data presented earlier (section on spectral analysis) using the Haar transform. Wavelet transforms were calculated for four one-dimensional data sets, at 10, 15, 20, and 25 m distance from the sonar transducer. The acoustical data were integrated over a 1.5 m distance, with structure occurring at smaller scales averaged out. Due to sampling and transect limitations, the maximum scale resolved was 24 m. All four transects showed dominance of patches at ≤ 6 m, as determined by the wavelet variance function, and in agreement with the results of the spectral analysis. However, there was evidence, for the 25 m data set, that patches appear to occur at two scales, ≤ 6 m and ≥ 22 m. This may be interpreted as suggesting that at least two different mechanisms are operating to create structure at two different scales. For example, at the smaller scales, krill behavior, such as swarming, may dominate and control the observed spatial structure. At the larger scales, other physical or biological processes may dominate patch formation. Given the present data constraint this is only speculative, but it illustrates the uses of these methods.

The two-dimensional representation of the data (distance on horizontal axis and scale on the vertical axis) provide information on the intensity of the variance with scale and position along the transect (Figure 7). The wavelet transform thus suggests higher-order structure. For a clear picture of higher-order structure (≥ 24 m) we require longer acoustic transects (i.e., larger data sets). With the present data constraint, it is difficult to determine whether a nested structure is present.

Multivariate Methods

We turn now to the multivariate systems in which the data are abundances of categories (cover-types, taxa, or life-forms), with an explicit spatial reference for each subsample. Commonly, subsamples are arranged in a grid and the data can be represented as a three-dimensional matrix in which the first two dimensions are spatial coordinates and the third one, the array of categories. There are two fundamental ways to look at the variation of pattern.

How the statistical descriptors of the landscape vary. This has been popular among ecologists since Greig-Smith (1957), although several drawbacks to this particular method have been pointed out (Upton and Fingleton 1985). With the indices described below, these drawbacks can be avoided (i) if the basic subsamples used for computing are randomly located in the grid, (ii) if the maximum sample size to analyze is restricted to be less than half the whole area side, and (iii) if boundary effects are avoided. Plots of averages and/or variances, since they are equally important, calculated for each cell, versus cell size are made. However, these methods do not consider spatial scales explicitly.

How indices vary between two grid cells separated by a distance d as this distance increases. The general procedure consists of randomly placing a dipole of length d n times on the grid, recording values at both extremes, and computing one of the following indices.

The dipole length, d , is increased (to a maximum of $1/2$ the minimum side of the grid to avoid boundary effects) and the index re-computed. Distances can be the ordinary euclidean or be arbitrarily defined.

The contingency table for length d is built with the co-occurrence frequencies of the species recorded at the cells intersected by the dipole's extremes. The same statistics described above can be applied to these contingency tables.

In the case of multivariate dissimilarity, the procedure is similar to the semivariogram, but a multivariate dissimilarity is substituted for the squared difference (Mackas 1984).

The Mantel index is defined as

$$\sum (X_{ij} - Y_{ij}) \quad (3)$$

where X_{ij} is the dissimilarity between cells i and j , and Y_{ij} is the corresponding distance. It tests the independence of both matrices. Well-documented ecological applications can be found in Upton and Fingleton (1985), Sokal (1986), Oden and Sokal (1986), and Legendre and Fortin (1989). The Mantel index can be presented in spectral form ("Mantel correlogram" in Legendre and Fortin 1989) to explore the relationship between dissimilarity and distance.

Empirical Orthogonal Functions

Empirical orthogonal functions (EOF) are also referred to as PCA (Principal Component Analysis) or Proper Orthogonal Decomposition. PCA is a tool extensively used for analysis of the spatial/temporal variability of physical fields (Preisendorfer 1988) such as winds, and of sea surface temperature (SST). An attempt to correlate physical fields (SST) and biological patchiness (pigment concentrations) will be the basis for the example presented herein. The technique is used to look at the aggregation of the variance to explain the spatial (temporal) structure. The data need only consist of real numbers.

The analysis reduces the dimensionality of the data, grouping the variance of the data to examine characteristics of induced or autonomous variables in the description of patchiness. A review by Matta and Marshall (1984) expands on the advantages of using PCA to examine phytoplankton variation.

Examples from biological oceanography: Sea surface temperature and water color (satellite). Oceanographic features such as warm core rings (WCR) are defined as distinctive patches for the purposes of this case study. WCR are clockwise rotating features, with Sargasso Sea water in the center, which have broken away from the meandering Gulf Stream.

Color data are from the Coastal Zone Color Scanner (CZCS), and sea surface temperature (SST) are from the Advanced Very High Resolution Radiometer (AVHRR). A total of 13 (single) ocean color images and 13 (single) matching SST images,¹ irregularly spaced in time but matching pairs within 24 hours, were used for the EOF analysis. These were processed using the Miami DSP image processing system for the VAX. NASA's SEAPAK-PC package and MATLAB were used for data extraction and manipulation.

¹The CZCS sensor is described by Hovis et al. (1980). Pigment concentrations are estimated following details given by Gordon et al. (1980) and Gordon and Morel (1983).

The images covered the period from March 31 to June 9, 1982. The area of interest, the Mid-Atlantic Bight, includes the shelf and slope between 35° and 42° North. The WCR under study was formed early in 1982 (Celone and Price 1983). The ring measured about 200 km in diameter (Figure 8).

Data were extracted from the images in a 100 x 100 pixel array, from 4 km resolution data, whose center changed as the WCR moved in a southwesterly direction. The two-dimensional data sets lend themselves to a Principal Component Analysis (PCA). Due to the small number of images, the 100 x 100 matrix was divided into a 3 x 4 matrix (12 bins). To assure full complement of positive eigenvalues for the covariance matrix, the

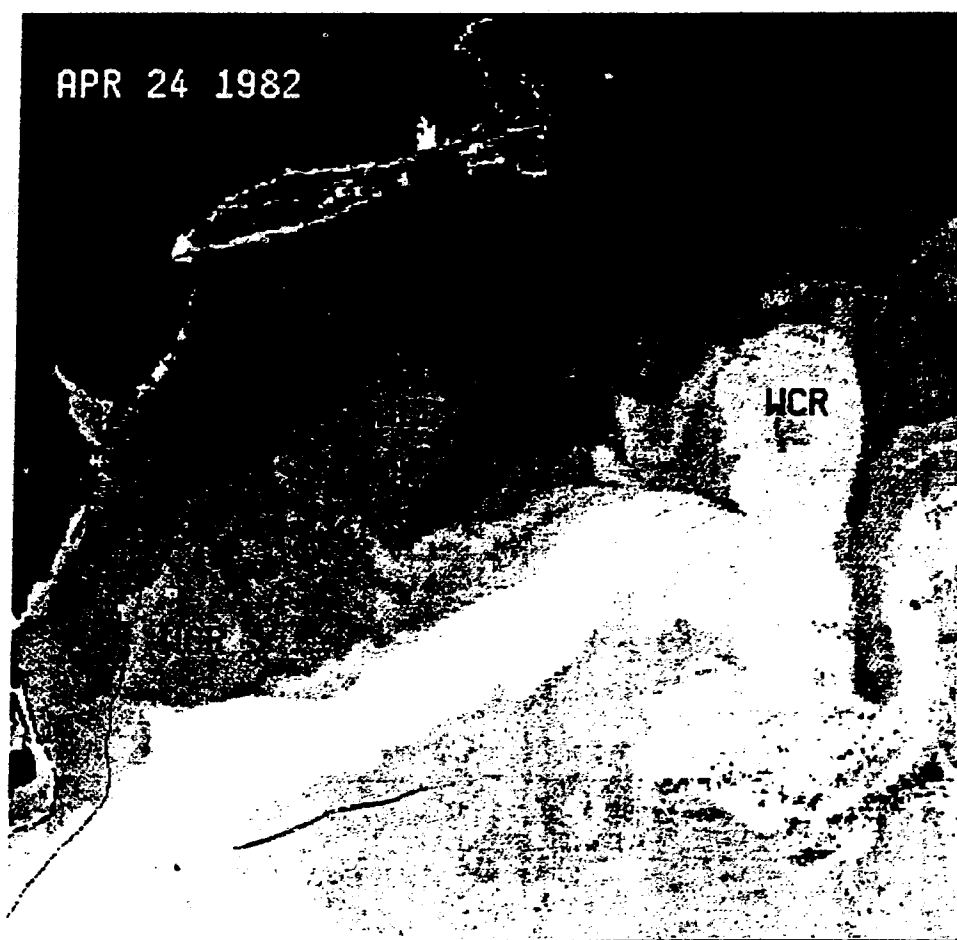


Figure 8. Satellite image of the Mid-Atlantic Bight (4 km resolution) for April 24, 1982. Three warm core rings (WCR) are shown. The WCR under use in the EOF analysis is shown in the center.

number of bins must be less than the number of images (Jassby et al. 1990). Once the $n \times p$ matrix was obtained (n = days, p = variable, mean temperature or pigment concentration per box), the covariance was calculated (yielding a square matrix) and the eigenfunction obtained from the covariance matrix. The mean is removed from all values to determine the anomalies in pigment concentrations and temperature. No rotation of eigenvectors was carried out.

The contour plot of the first eigenvector is shown in Figure 9, as an example of the patterns observed in the satellite images. The standard deviation showed greater variability in the outside of the rings.

Table 3 shows the total variance (as a percentage) explained by the PCs. About 90% of the variability is explained by the first eigenvector in the pigment data. The first eigenvector explains about 80 - 85% of the variance in the temperature field. To pull out more modes, a larger data set is needed.

The most important point of the exercise is to demonstrate ways in which moving spatial features can be tracked in the ocean. The technique reveals recognizable patterns (anomalies) in both the SST and pigment fields. In addition, it allows for the inference of mechanisms (e.g., advection) that may be responsible for the variability observed.

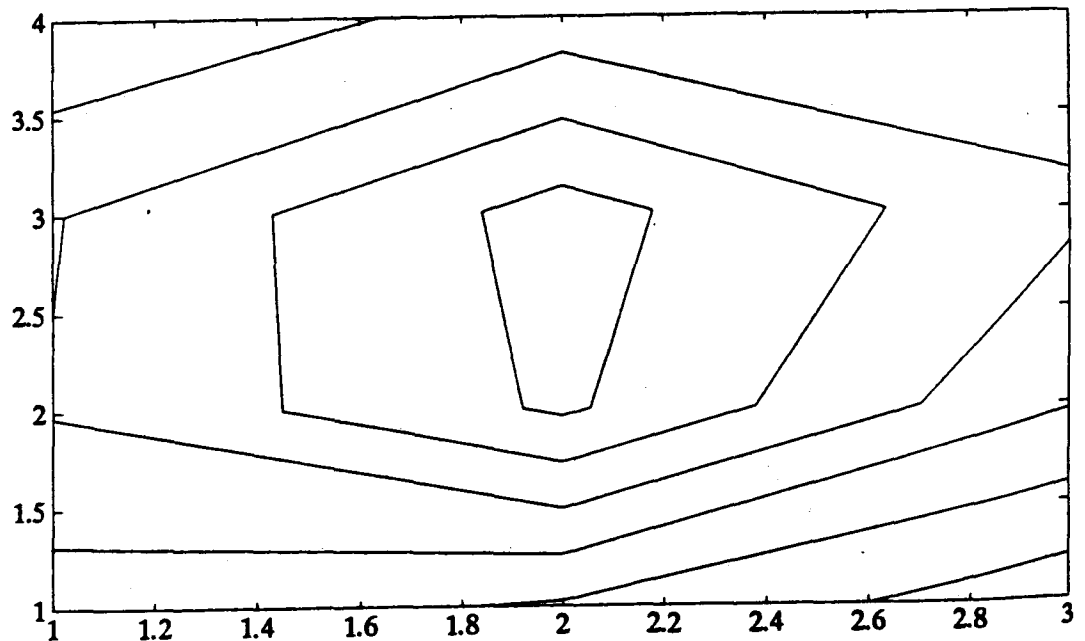


Figure 9. Contour plot of first eigenvector for sea-surface temperature (SST) showing lows in center and highs toward the bottom right-hand corner of the plot.

Table 3. Percentage total variance explained by the first most important principal components (PC) of temperature (SST) and pigment concentration (PIG) of a warm-core ring.

PC	SST	PIG
1	84.2	89.8
2	7.1	5.0
3	4.9	2.9
4	4.3	1.2

Fractal Geometry: Applications in Analysis and Description of Patch Patterns and Patch Dynamics

Mandelbrot's concept of a fractal extends our usual ideas of classical geometry beyond those of point, line, circle into the realm of the irregular, disjoint, and singular (Mandelbrot 1983) and so provides us with a new way to understand and analyze spatial phenomena. Fractals are shapes in which an identical motif repeats itself on an ever-diminishing scale. A fractal is a non-integer dimension.

For ecological applications, Krummel et al. (1987) used fractal models to examine how patch boundary varies with patch size. The relationship is applied to landscape patches by the equality between area and perimeter length,

$$A = BL^D$$

where A is patch area, L is the patch perimeter, B is a constant, and D is the fractal dimension. By using data for patch area and patch perimeter, and relationships

$$\log A = \log B + D \log L$$

we can estimate the fractal dimension D.

The fractal characteristics over a landscape may be important measures in ecological diversity, stability, and function. Many recent studies have included measures of the fractal geometry of landscapes and patch patterns (Burrough 1981, 1983; Krummel et al. 1987, Gardner et al. 1987, Milne 1988, O'Neill et al. 1988, DeCola 1989, Wiens and Milne 1989, Rex and Malanson 1990, Williamson and Lawton 1991).

Recently, Milne (1990) and Sugihara and May (1990) reviewed fractal applications in ecological research and landscape. Here, we shall select some interesting aspects associated with spatial patterns and patch dynamics and introduce them as follows.

Patch hierarchical scaling. Different observational scales capture different aspects of structure, and these transitions are signaled by shifts in apparent fractal dimension of the

object. This suggests an interesting application of fractals as a method for distinguishing hierarchical size scales of patches in nature; for example, to determine boundaries between hierarchical levels, or the scaling rules for extrapolation within each level.

Bradbury et al. (1984) examined the possibility of hierarchical scaling in an Australian coral reef. They used the dividers method (Mandelbrot 1983) in transects across the reef to determine whether D depends on the range of length scales. They found that three ranges of scale correspond nicely with the scales of three major reef structures: 1 - 10 cm corresponds to the size of anatomical features within individual coral colonies; 20 - 200 cm corresponds to the size range of whole adult living colonies; and 5 - 10 m is the size range of major geomorphological structures. This showed that the shifts in D at different spatial scales appear to signal where the boundaries occur in the hierarchical organization of reefs.

Fractal spatial patterns and modified Brownian dynamics (diffusion). Hastings et al. (1982) and Mandelbrot (1983) have discussed how fractal exponents may be incorporated into diffusion processes, as a scaling factor for normalizing increments in space and time. They find that D may be used as an index of succession in circumstances where simple patch-extinction models are reasonable. A recent study has showed that many of nature's seemingly patchy shapes can be effectively characterized and modeled as random fractals based upon generalizations of fractional Brownian motion (Voss 1988).

DISCUSSION

It is worthwhile to recap the concepts of Kotliar and Wiens (1990) on the scales of patchiness. Recognition of spatial pattern is dependent on the scale of observation as well as on the scales of the processes under study. It is the coupling of pattern and process (i.e., patch dynamics) at different scales, be it autonomous or induced, that leads to the subjectivity involved with describing patchiness. Heterogeneity is recognized not only in terms of the processes affecting the variability of patches, but also in the changes that occur due to this variability. The description and analysis of patchiness is thus limited by the techniques for observation, sampling, and analysis. The problem is to derive methods for statistically recognizing spatio-temporal pattern. The examples used in this chapter are representative of the techniques available. The techniques allow for inferences regarding interactions between the physical and biological phenomena creating pattern at various scales. The causes and mechanisms of patch formation are discussed by Deutschman et al. (this volume) and demonstrate the complexity of these interactions.

In view of the above discussion, we might conclude that simple comparisons between terrestrial and marine systems are often artificial. Differences in scale are inherent properties of the systems and must be considered. Better comparisons of techniques across scales and ecosystems are needed. This perspective seems appropriate when we realize that all terrestrial and marine ecosystems are tightly coupled and our ecological perspective is expanding to an all-inclusive global outlook.

ACKNOWLEDGMENTS

The authors would like to thank Drs. S.A. Levin, T. Powell, and J. Steele for their kind invitation and encouragement. The authors would also like to thank all the people who were involved in the development of this chapter!

REFERENCES

- Abbott, M.R. (This volume.). Phytoplankton patchiness: Ecological implications and observation methods.
- Argoul, F., A. Arneodo, G. Grasseau, Y. Gagne, E.J. Hopfinger, and U. Frisch. 1989. Wavelet analysis of turbulence reveals the multi-fractal nature of the Richardson cascade. *Nature* 338: 51-53.
- Barale, V. 1987. Remote observations of the marine environment: Spatial heterogeneity of the mesoscale ocean color field in CZCS imagery of California near-coastal waters. *Remote Sensing of the Environment* 22: 173-186.
- Barale, V., and C.C. Trees. 1987. Spatial variability of the ocean color field in CZCS imagery. *Advances in Space Research* 7(2): 95-100.
- Barry, J.P., and P.K. Dayton. 1991. Physical heterogeneity and the organization of marine communities. In: J. Kolasa and S.T.A. Pickett (eds.). *Ecological Heterogeneity*. Springer-Verlag, New York.
- Bradbury, R.H., R.E. Reichelt, and D.G. Green. 1984. Fractals in ecology: Methods and interpretation. *Marine Ecology Progress Series* 14: 295-296.
- Bradshaw, G.A. 1991. Hierarchical pattern and process in Douglas-fir forests using wavelet analysis. Ph.D. Dissertation. Oregon State University, Corvallis, OR.
- Bradshaw, G.A., and T.A. Spies. In press. Characterizing forest canopy structure using wavelet transform. *Journal of Ecology*.
- Burrough, P.A. 1981. Fractal dimensions of landscapes and other environmental data. *Nature* 294: 241-243.
- _____. 1983. Multiscale sources of spatial variation in soil: I. Application of fractal concepts to nested levels of soil variations. *Journal of Soil Science* 34: 577-597.
- Celone, P.J., and C.A. Price. 1983. Anticyclonic warm-core Gulf Stream rings off the northeastern United States during 1982. *Annales Biologiques* 39: 19-23.
- Chatfield, C. 1984. *The Analysis of Time Series: An Introduction*. Chapman and Hall, NY.
- Daubechies, I. 1988. Orthogonal basis of compactly supported wavelets. *Communications of Pure and Applied Mathematics* 41: 909-996.
- DeCola, L. 1989. Fractal analysis of a classified landsat scene. *Photogrammetric Engineering and Remote Sensing* 55: 601-610.
- Denman, K.L. (This volume.) The ocean carbon cycle and climatic change: An analysis of interconnected scales.
- Denman, K., and T. M. Powell. 1984. Effects of physical processes on planktonic ecosystems in the coastal ocean. *Oceanography and Marine Biology Annual Review* 22: 125-168.
- Deutschman, D., G.A. Bradshaw, W.M. Childress, K. Daly, D. Grünbaum, M. Pascual, N. Schumaker, and J. Wu. (This volume.) Mechanisms of patch formation.
- Downing, J.A.. 1991. Biological heterogeneity in aquatic ecosystems. In: J. Kolasa and S.T.A. Pickett (eds.). *Ecological heterogeneity*. Springer-Verlag, New York.
- Forman, R.T.T., and M. Godron. 1986. *Landscape Ecology*. Wiley, New York.
- Gamage, N.K.K. 1990. Detection of Coherent Structures in Shear Induced Turbulence Using the Wavelet Transform Methods. AMS Symposium on Turbulence and Diffusion. Roskilde, Denmark, April 1990.
- Gardner, R.H., B.T. Milne, M.G. Turner, and R.V. O'Neill. 1987. Neutral models for the analysis of broad-scale landscape pattern. *Landscape Ecology* 1: 19-28.
- Gordon, H.R. and A.G. Morel. 1983. *Remote Assessment Ocean Color for Interpretation of Satellite Visible Imagery: A Review*. Springer-Verlag, New York.
- Gordon, H.R., D.K. Clark, J.L. Muller, and W.A. Hovis. 1980. Phytoplankton pigments from the Nimbus-7 Coastal Zone Color Scanner: Comparisons with surface measurements. *Science* 210: 63-66.
- Greene, C.H., E.A. Widder, M.J. Youngbluth, M. Tamse, and G.E. Johnson. (In press). The fine structure, migration behavior, and bioluminescent activity of krill sound-scattering layers. *Limnology and Oceanography*.
- Greig-Smith, P. 1957. *Quantitative Plant Ecology*. Academic Press, New York.
- Grünbaum, D. 1991. Three unrelated projects in mathematical biology. Ph.D. Dissertation. Univ. of Washington, Seattle, WA.
- Hamner, W.M. 1988. Behavior of plankton and patch formation in pelagic ecosystems. *Bulletin of Marine Science* 43(3): 752-757.
- Hastings, H.M., R. Pkelney, R. Monticciolo, D.V. Kannon, and D.D. Monte. 1982. Time scales, persistence

- and patchiness. *Biosystems* 15: 281-289.
- Haury, L.R., J.A. McGoan, and P.H. Wiebe. 1978. Patterns and processes in the time-space scales of plankton distributions. In: J.H. Steele (ed.). *Spatial patterns in plankton communities*. Plenum Press, New York.
- Hovis, W.A., D.K. Clark, F. Anderson, R.W. Austin, W.H. Wilson, E.T. Baker, D. Ball, H.R. Gordon, J.L. Muller, S.Z. El-Sayed, B. Strum, R.C. Wrigley, and C.S. Yentsch. Nimbus-7 Coastal Zone Color Scanner: System description and initial imagery. *Science* 210: 60-63.
- Issacs, J.D. 1977. The life of the open sea. *Nature* 267: 778-780.
- Jassby, A.D., and T.M. Powell. 1990. Detecting changes in ecological time series. *Ecology* 71(6): 2044-2052.
- Jassby, A.D., T.M. Powell, and C.R. Goldman. 1990. Interannual fluctuations in primary production: Direct effects and the trophic cascade at Castle Lake, California. *Limnology and Oceanography* 35(5):1021-1038.
- Kolasa, J. and S.T.A. Pickett (eds.). 1991. *Ecological Heterogeneity*. Springer-Verlag, New York.
- Kotliar, N.B., and J.A. Wiens. 1990. Multiple scales of patchiness and patch structure: A hierarchical framework for the study of heterogeneity. *Oikos* 59: 253-260.
- Krummel, J.R., R.H. Gardner, G. Sugihara, R.V. O'Neill, and P.R. Coleman. 1987. Landscape patterns in disturbed environment. *Oikos* 48: 321-324.
- Legendre, L., and S. Demers. 1984. Towards dynamic biological oceanography and limnology. *Canadian Journal of Fishery Aquatic Science* 41(1): 2-19.
- Legendre, L., and P. Legendre. 1983. *Numerical Ecology*. Elsevier, Amsterdam.
- Legendre, P., and M.-J. Fortin. 1989. Spatial pattern and ecological analysis. *Vegetatio* 80: 107-138.
- Levin, S.A. 1990. Physical and biological scales and the modelling of predator-prey interactions in large marine ecosystems. In: K. Sherman, L.M. Alexander, and B.D. Gold (eds.). *Large Marine Ecosystems: Patterns, Processes, and Yields*. AAAS, Washington, DC.
- Lloyd, M. 1967. Mean crowding. *Journal of Animal Ecology* 36: 1-30.
- Mackas, D.L. 1984. Spatial autocorrelation of plankton community composition in a continental shelf ecosystem. *Limnology and Oceanography* 29(3): 451-471.
- Mackas, D.L., K.L. Denman, and M.R. Abbott. 1985. Plankton patchiness: Biology in the physical vernacular. *Bulletin of Marine Science* 37(2): 652-674.
- Mallat, S.G. 1988. Review of Multi-frequency Channel Decompositions of Images and Wavelet Models. Robotics report no. 178, Courant Institute of Mathematical Sciences, New York University, New York.
- Mandelbrot, B.B. 1983. *The Fractal Geometry of Nature*. W.H. Freeman and Company, New York.
- Marquet, P.A., M.-J. Fortin, J. Pineda, D.O. Wallin, J. Clark, Y. Wu, S. Bollens, C.M. Jacobi, and R.D. Holt. (This volume). Ecological and evolutionary consequences of patchiness: A marine-terrestrial perspective.
- Matta, J.F. and H.G. Marshall. 1984. A multivariate analysis of phytoplankton assemblages in the western North Atlantic. *Journal of Plankton Research* 6(4): 663-675.
- Milne, B.T. 1988. Measuring the fractal geometry of landscapes. *Applied Mathematics and Computation* 27: 67-79.
- _____. 1990. Lessons from applying fractal models to landscape patterns. In: M.G. Turner and R.H. Gardner (eds.). *Quantitative Methods in Landscape Ecology*. Springer-Verlag, New York.
- O'Neill, R.V., B.T. Milne, M.G. Turner, and R.H. Gardner. 1988. Resource utilization scales and landscape pattern. *Landscape Ecology* 2: 63-69.
- Oden, N.L., and R.R. Sokal. 1986. Directional autocorrelation: An extension of spatial correlograms to two dimensions. *Systematic Zoology* 35: 608-617.
- Paine, R.T., and S.A. Levin. 1981. Intertidal landscapes: Disturbance and the dynamics of pattern. *Ecological Monographs* 5: 145-178.
- Parsons, T.R. 1976. The structure of life in the sea. In: D.H. Cushing and J.J. Walsh (eds.). *The Ecology of the Seas*. Blackwell Scientific Publications, Oxford.
- Pickett, S.T.A., and P.S. White. 1985. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, Orlando, Florida.
- Platt, T., and K.L. Denman. 1975. Spectral analysis in ecology. *Annual Review of Ecology and Systematics* 6: 189-210.

- Powell, T.M. 1989. Physical and biological scales of variability in lakes, estuaries, and the coastal ocean. In: J. Roughgarden, R.M. May, and S.A. Levin (eds.). *Perspectives in Ecological Theory*. Princeton University Press, Princeton, New Jersey.
- Preisendorfer, R.W. 1988. *Principal Component Analysis in Meteorology and Oceanography*. Elsevier, New York.
- Pringle, C.M., R.J. Naiman, G. Bretschko, J.R. Karr, M.W. Oswood, J.R. Webster, R.L. Welcomme, and M.J. Winterbourn. 1988. Patch dynamics in lotic systems: The stream as a mosaic. *Journal of the North American Benthological Society* 7: 503-524.
- Rex, K.D., and G.P. Malanson. 1990. The fractal shape of riparian forest patches. *Landscape Ecology* 4: 249-258.
- Sokal, R.R. 1986. Spatial data analysis and historical processes. In: E. Diday et al. (eds.). *Data Analysis and Informatics*. IV Proc. 4th Intl. Sym. Data Anal. Informatics (Versailles, France, 1985). North Holland, Amsterdam pp. 29-43.
- Steele, J. H. (ed.). 1978. *Spatial Pattern in Plankton Communities*. Plenum Press, New York.
- Steele, J. H. 1985. A comparison of terrestrial and marine ecological systems. *Nature* 313: 355-358.
- _____. 1989. The ocean landscape. *Landscape Ecology* 3(3/4): 185-192.
- Stommel, H. 1963. Varieties of oceanographic experience. *Science* 139: 572-576.
- Sugihara, G., and R.M. May. 1990. Applications of fractals in ecology. *TREE* 5: 79-86.
- Turner, M.G., and R.H. Gardner (eds.). 1991. *Quantitative Methods in Landscape Ecology*. Springer-Verlag, New York.
- Upton, G.J.G., and B. Fingleton. 1985. *Spatial Data Analysis by Example*. Vol. I: Point Pattern and Quantitative Data. John Wiley & Sons, Chichester.
- van Es, H. (This volume). The spatial nature of soil variability and its implications for field studies.
- Voss, R.F. 1988. Fractals in nature: From characterization to simulation. In: H. Peitgen and D. Saupe (eds.). *The Science of Fractal Images*. Springer-Verlag, New York.
- Weber, L.H., S.Z. El-Sayed, and I. Hampton. 1986. The variance spectra of phytoplankton, krill and water temperature in the Antarctic Ocean South of Africa. *Deep-Sea Research* 33: 1327-1343.
- Wiens, J.A. 1976. Population responses to patchy environments. *Annual Review of Ecology and Systematics* 7: 81-120.
- Wiens, J.A., and B.T. Milne. 1989. Scaling of "landscapes" in landscape ecology, or, landscape ecology from a beetle's perspective. *Landscape Ecology* 3: 87-96.
- Williamson, M.H., and J.H. Lawton. 1991. Fractal geometry of ecological habitats. In: S.S. Bell, E.D. McCoy, and H.R. Mushinsky (eds.). *Habitat Structure*. Chapman and Hall, London, pp. 69-86.