Analysis and modeling of scale-invariance in plankton abundance

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Abstract

The power spectrum, $S$, of horizontal transects of plankton abundance are often observed to have a power-law dependence on wavenumber, $k$, with exponent close to $-2$: $S(k) \propto k^{-2}$ over a wide range of scales. I present power spectral analyses of aircraft lidar measurements of phytoplankton abundance from scales of 1 to 100 km. A power spectrum $S(k) \propto k^{-2}$ is obtained. As a model for this observation, I consider a stochastic growth equation where the rate of change of plankton abundance is determined by turbulent mixing, modeled as a diffusion process in two dimensions, and exponential growth with a stochastically variable net growth rate representing a fluctuating environment. The model predicts a lognormal distribution of abundance and a power spectrum of horizontal transects $S(k) \propto k^{-1.8}$, close to the observed spectrum. The model equation predicts that the power spectrum of variations in abundance in time at a point in space is $S(f) \propto f^{-1.5}$ (where $f$ is the frequency). Time series analysis of local variations of phytoplankton and zooplankton yield a power-law power spectrum with exponents $-1.3$ and $-1.2$, respectively from time scales of one hour to one year. These values are roughly consistent with the model prediction of $-1.5$. The distribution of abundances is nearly lognormal as predicted. The model may be more generally applicable than for the spatial distribution of plankton. I relate the model predictions to observations of spatial patchiness in vegetation.
Levin (1992) has argued that the central problem in ecology is the determination of the factors controlling the spatial pattern of ecosystems at the wide range of scales at which spatial heterogeneity is observed. Particularly intriguing is how movement and interactions at small scales, such as competition, dispersal, and local environmental variations, can result in spatial pattern at larger scales.

Several generic mechanisms have been proposed to generate spatial variations in abundance. For instance, diffusive instabilities in multiple species models can generate complex spatial patterns (Okubo 1974, Levin and Segel 1976). Roughgarden (1977) has argued that random fluctuations in resources necessary for reproduction may also generate complex, patchy spatial distributions. In this paper we propose a model for spatial heterogeneity based on the second mechanism: dispersal in a stochastic environment. The model is an extension of the classic equation studied by Kierstead and Slobodkin (1953) and Skellam (1951) with diffusive dispersal and exponential growth with the net growth rate, or production efficiency, a stochastic variable in space and time. I report on the model behavior in space and time and compare the predictions to observations of spatial and temporal variations in plankton abundance.

Plankton systems are uniquely valuable for the analysis and modeling of spatial variations in abundance because remote sensing techniques make possible high-resolution measurements in space and time over a wide range of scales. Power spectra of one-dimensional transects of phytoplankton and zooplankton abundance have been generally found to be a power-law function of wavenumber with an exponent close to $-2$: $S(k) \propto k^{-2}$ where $S$ denotes the power spectrum (Horwood 1978; Platt and Denman 1975; Mackas and Boyd 1979; Denman and Abbott 1988). There are differences in the reported spectra. Platt and Denman (1975) argued that a crossover exists in their data from a high wavenumber region with exponent $-2$ to a lower wavenumber region with exponent $-\frac{5}{3}$. The transition occurs at a spatial scale of about 10 m. Horwood (1978) found no such crossover. He also analyzed variations on much larger scales, up to 20 km. He found that the power spectral behavior with exponent $-2$ continued up to these scales. This is consistent with the results
of Denman and Abbott (1988) who found $S(k) \propto k^{-2}$ from scales of 1 to 100 km with ocean color data.

I have carried out power spectral analyses of phytoplankton abundance estimated with measurements taken by the Airborne Lidar Observatory. I used 23 transects, about half of which were sampled in the continental shelf off the coast of Maryland and half in the Arabian Sea. The power spectrum of each transect was estimated as the modulus squared of the Fast Fourier Transform. Each of the spectra were then averaged at equal frequency values. The resulting average spectrum is presented in Figure 1. The straight line in the plot represents the form of the power-law spectrum $S(k) \propto k^{-2}$. A good fit is obtained except for the largest scales where the variance falls below the scale-invariant trend. I found no significant difference in spectra between transects parallel and perpendicular to the coast. These results are consistent with the results of power spectral analysis of Denman and Abbott (1988) who found a $S(k) \propto k^{-2}$ spectrum over the same scales with ocean color data.

Several models have been proposed to explain this spectrum. Denman, Okubo, and Platt (1977) proposed three different regimes for the power spectrum based on the relative importance of turbulent mixing and the rate of reproduction. Their spectrum predicts that the power spectrum should decrease sharply below a characteristic wavenumber. The continual increase of the power spectrum at decreasing wavenumbers observed in my analysis and the others I have cited appears to invalidate this prediction.

Fasham (1978) has simulated a number of stochastic models that give rise to power spectra similar to $S(k) \propto k^{-2}$. Fasham begins by presenting an extension of the equation first studied by Kierstead and Slobodkin (1953) and Skellam (1951) representing the abundance of a species in time and space with turbulent dispersion modeled by the diffusion equation and exponential growth with a constant growth rate. The original equation in one spatial dimension is

$$\frac{\partial a}{\partial t} = D \frac{\partial^2 a}{\partial x^2} + \alpha a$$

where $a$ is the local abundance and $\alpha$ is the growth rate. Fasham (1978) extended this
equation by including a Gaussian white noise $\eta(x,t)$ to represent a fluctuating environment. The resulting equation is
\[
\frac{\partial a}{\partial t} = D \frac{\partial^2 a}{\partial x^2} + \alpha a + \eta(x,t)
\] (2)
This equation generates a spatial distribution with a power spectrum $S(k) \propto (Dk^2 + |\alpha|)^{-1}$. At high wavenumbers this power spectrum is $S(k) \propto k^{-2}$, similar to the spectrum often observed. However, this equation describes dynamics in one dimension only. As such, it is an inappropriate model for dynamics of phytoplankton on the ocean surface where a two or three dimensional model is appropriate. The above equation, generalized to two dimensions, has been used to model the height of a surface on which grains of sand are randomly deposited in space and time. The power spectrum of one-dimensional transects of the surface generated by the model is not a power-law function (Edwards and Wilkinson 1982). Fasham’s model therefore does not explain the $S(k) \propto k^{-2}$ spectrum.

In this paper I will consider another extension of the diffusion equation with exponential growth. In the model I include the effects of a fluctuating environment by making the net growth rate or production efficiency a random function in space and time. Allowing the production efficiency to vary may better reflect the effects of a variable environment than a random forcing term uncoupled to the abundance. Many complex processes are thought to affect the production efficiency of phytoplankton: nitrate upwelling and downwelling (Powell and Richerson 1985), fluctuations in light intensity caused by internal waves (Abbott, Powell, and Richerson 1982), and temperature fluctuations (Denman 1976). In this paper I will model environmental variations resulting in variations in production efficiency in the simplest manner possible: as a Gaussian white noise in space and time. I consider the equation in two spatial dimensions, as applicable for plankton on the ocean surface. The model equation is
\[
\frac{\partial a}{\partial t} = D \nabla^2 a + \eta(x, y, t)a
\] (3)
I will compare abundances generated by this equation to previous studies of spatial heterogeneity in plankton and my analysis of phytoplankton heterogeneity in space and time with
The above equation has been well studied in the physics literature where it is a variant of the Kardar-Parisi-Zhang (KPZ) equation (Kardar, Parisi, and Zhang 1986). The KPZ equation was originally proposed to model the fractal characteristics of atomic surfaces grown by ion deposition. The KPZ equation in two spatial dimensions for a surface with elevation $h(x, y, t)$ is

$$\frac{\partial h}{\partial t} = D \nabla^2 h + \lambda (\nabla h)^2 + \eta(x, y, t)$$

(4)

The surface generated by this equation has one-dimensional transects with a Gaussian distribution and power spectra $S(k) \propto k^{-1.8}$ (Amar and Family 1990, Moser, Wolf, and Kertesz 1991). The model also has local variations in time with a power spectrum $S(f) \propto f^{-1.5}$.

With the transformation $a = exp(\frac{\lambda}{D}h(x, y, t))$ the above equation becomes (Kardar, Parisi, and Zhang 1986)

$$\frac{\partial a}{\partial t} = D \nabla^2 a + \lambda \frac{\lambda}{D} \eta(x, y, t)a$$

(5)

which is the same as equation (3) except for the multiplicative factor in the stochastic term. This factor does not change the form of the power spectra since the spectra are independent of the variance of the noise term $\eta(x, y, t)$.

The spectral behavior of the solution to the Kardar-Parisi-Zhang equation can be used to determine the behavior of equation (5). Since the Kardar-Parisi-Zhang equation generates a Gaussian distribution and equation (5) has been obtained by an exponential transformation, the distribution of abundances generated by equation (5) will be lognormal. The power spectra of variations in abundance in space and time will be the same as those of the Kardar-Parisi-Zhang equation. This conclusion is based on the power spectral analyses of Gomes da Silva and Turcotte (1994) with Gaussian and lognormal noises with power-law power spectra. These authors found that the form of the spectra are unchanged after an exponential transformation unless the data are extremely skewed. The power spectrum of horizontal transects, $S(k) \propto k^{-1.8}$ is close to the observed spectrum with an exponent close to $-2$ from scales of meters to hundreds of kilometers.
To test the model prediction of local variations in time, we have obtained time series of local phytoplankton and zooplankton abundance off the coast of Maryland sampled hourly up to time scales of one year from Wirick (1996). The data series are described in Ascioti et al. (1993) where the authors tested the hypothesis that chaos may explain the aperiodic fluctuations in local abundance observed in the time series. Although their results did not conclude the presence of chaos, they suggested that nonlinear dynamics may account for at least some of the variability in the data. In Figure 2 we present the cumulative distribution function (thick lines) of the data to test the model prediction of a lognormal distribution. The thin lines represent the cumulative lognormal distribution fit to the data. Reasonably good fits are obtained. The power spectra of each of the series are presented in Figure 3. Both series exhibit a good fit to a power-law relationship with exponents -1.3 and -1.2 for phytoplankton and zooplankton, respectively. These values are close to the exponent -1.5 predicted by the model equation (5).

The model I have introduced may be more generally applicable than for plankton. The terms in the model equation (5) may describe aspects of growth and dispersal applicable to terrestrial species. Diffusion is a common parameterization for dispersal in terrestrial species. Karieva (1983) has used the diffusion equation to model insect dispersal. Hengeveld and Haeck (1982) have analyzed the spatial distribution of variety of species and found that species generally have a maximum abundance at the center of their range with abundance tapering off at the edges of the range. A diffusion model of dispersal or migration is consistent with this general biogeographical rule and is one of the models the authors propose to explain their observations (Hengeveld and Haeck 1981). In the first application of the diffusion model to dispersal, Skellam (1951) applied the model to the colonization of species as diverse as muskrats and oak trees. The other term in the equation, exponential growth in a fluctuating environment, may also be generally applicable for “opportunistic” species for which the environmental fluctuations are strong enough that the species abundance rarely approaches the local carrying capacity. For species whose abundance is often close to the local carrying capacity, exponential growth is inappropriate and the logistic growth terms must be used.
The model we have studied predicts a lognormal distribution of abundance as generally observed for species in a wide range of habitats (Preston 1962, May 1975). A number of quantitative studies of patchiness in vegetation have been performed. The results of these investigations are consistent with the spatial power spectrum \( S(k) \propto k^{-2} \). These will be discussed after a brief discussion of fractal geometry.

Topography is a useful analog for the variations in the abundance of phytoplankton and zooplankton on the ocean surface. The analogy is useful for introducing fractal aspects of the model and their possible relation to vegetation patchiness analyzed with fractal measures. The power spectrum of topography generally has a power-law dependence \( S(k) \propto k^{-2} \) (Fox and Hayes 1985) as observed for plankton abundance. Topography is also a type example of a self-affine or fractal function. Introductory geology students learn that objects (a person, a hammer, or a coin) must be placed into many geological photographs in order to set the scale because topographic variations have no characteristic scale. An introduction to the application of fractal geometry in ecology is given by Sugihara and May (1990). There are three fractal aspects of the Earth’s topography. The Earth’s surface is generally self-affine with Hausdorff measure \( Ha = \frac{1}{2} \). The Hausdorff measure is defined by the relationship between the change in elevation, \( \Delta h \), in the case of topography, over a horizontal distance interval, \( \Delta x \): \( \Delta h \propto \Delta x^{Ha} \). Ahnert (1984) has found \( Ha \approx \frac{1}{2} \) from topographic maps. A random walk is another example of a function with Hausdorff dimension \( Ha = \frac{1}{2} \). Another measure of the fractal geometry of topography is given by the exponent of the power spectrum of one-dimensional transects. This measure, \( \beta \) is usually defined by the negative of the power spectral exponent: \( S(k) \propto k^{-\beta} \). For topography and plankton abundance, \( \beta \approx 2 \). \( Ha \) and \( \beta \) are related by the relation \( \beta = 1 + 2Ha \) (Turcotte 1992). The second fractal aspect of topography is that coastlines and contour lines are often fractal with dimension 1.25. On water-filled topography, a coastline is the connected subset of the topography at the constant elevation of sea level. Finally, the cumulative number of islands, domains of topography above a fixed elevation, greater than an area, \( A \), has a power-law dependence
on area with an exponent close to $-\frac{3}{4}$: $N(> A) \propto A^{-\frac{3}{4}}$ (Korcak 1938). A similar area distribution is observed for lakes (Maybeck 1995). Each of these fractal characteristics of topography have been identified in species abundance patterns. The power spectral analysis of phytoplankton and zooplankton has been discussed. Krummel et al. (1987) has calculated the fractal dimension of deciduous forest patches in the U. S. Geological Survey Natchez, Mississippi 1:250,000 Quadrangle. Although they emphasized the variation in perimeter fractal dimension between different scales, the fractal dimension varies only between about 1.2 for small scales and 1.4 for the larger scales. Given the statistical variation in the fractal dimension, these values are not inconsistent with a value of 1.25 as measured for coastlines. The cumulative frequency-area distribution of Cypress and Broadleaf patches in the Okefenokee Swamp was calculated by Hastings et al. (1982). They obtained exponents in the range of $-0.5$ to $-0.8$, similar to the exponent obtained in the cumulative distribution of islands and lakes. Collins and Glenn (1990) have identified similar scale-invariant or hierarchical patchiness in grasslands. Kondev and Henley (1995) have shown that two-dimensional fractal functions have fractal “coastlines” (defined as subsets of constant magnitude) and a power-law cumulative distribution of areas above a threshold magnitude (“islands”). They showed that there is a unique relationship between the fractal dimension of “coastlines,” the size distribution of “islands,” and the exponent $\beta$ in the power spectrum. As a result, similar values of the fractal dimension of “coastlines” and the size distribution of “islands” for topography and vegetation patches imply that the power spectra of variations in topography and species abundance along a transect are comparable. This suggests that the power spectrum of abundance variations in vegetation for the study areas above may be roughly consistent with the model power spectrum $S(k) \propto k^{-2}$. Palmer (1988) has performed variogram analysis of spatial variations in abundance in vegetative species. Although his results imply that the negative of the power spectral exponent, $\beta$, is generally smaller than 2 and exhibits considerable variability between species and habitats, he concluded that fractal geometry is a useful description of spatial variations in vegetative abundance. I hope that this
work stimulates the continued study of species abundance patterns with fractal geometry with particular emphasis on the universality of the fractal measures obtained.

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$S(k)$

$k$ (1/km)

slope = -2