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SMR/99-27

AUTUMN COURSE ON MATHEMATICAL ECOLOGY

(16 November - 10 December 1982)

PARTICLE SIZE SPECTRA IN ECOLOGY

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INTRODUCTION

The use of size distributions as descriptors of ecosystems goes back at least to Elton (1927), although quantitative applications have appeared only during the past decade. Elton noted that there was a characteristic difference between terrestrial and aquatic ecosystems; on land the organisms in the lower trophic levels tend to be larger than the organisms which feed on them (e.g., trees, giraffes, tigers), while in the sea the reverse is true (phytoplankton, zooplankton, fish). The value of this observation was dramatically emphasized by the advent of automated particle size measurement devices and their use in marine biology, which occurred in the 1960's (Sheldon and Parsons 1967). A Coulter counter was used on the 1970 circumnavigation of the western hemisphere by the Canadian research vessel Hudson, and this provided the first opportunity to compare particle size distributions from widely distributed pelagic marine environments, including both polar regions and the tropical waters of the Atlantic and Pacific oceans (Sheldon et al. 1972). This work greatly extended Elton's observation by showing that there are also patterns in the size distributions from temperate

and polar regions which are characteristically different from those found in tropical waters.

The results of the Hudson '70 cruise led to a flurry of interest in the nature of these patterns and how they arose, and it became evident that bioenergetic models based on the conservation of energy could explain the observed regularities (Kerr 1974, Sheldon et al. 1977, Platt and Denman 1977, 1978, Silvert and Platt 1978, 1980). Furthermore these models predicted that similar patterns should be found in freshwater systems, and size patterns have indeed been observed, although they are not as smooth as those found in offshore environments (Sprules et al. 1979). Since these models involve assumptions about the size structure of predator-prey relations it has usually been assumed that they would not apply in systems with different structures; for example, the size-dependence of feeding in many terrestrial and benthic environments is quite different from that found in the sea. Therefore even though patterns of size distribution had also been observed among bottom fauna (Ursin 1973, Thiel 1975), these were not usually expected to be as general or significant as those found in pelagic systems. It therefore came as a surprise to many workers in the field when Schwinghamer (1981) showed that benthic ecosystems exhibit regularities at least as pronounced as those found in pelagic systems, and that the same patterns are found in spatially separated systems with quite different community structure and bottom type. Although it was certainly recognized that other factors could be as important as food web structure in determining the size distributions of ecosystems (Smith 1976), there is no quantitative theory of how this occurs, and the absence of such a theory has left many ecologists with the feeling that such patterns must be vague and qualitative. Since these benthic results indicate that the patterns are quite sharp and predictable, it seems that theoretical ecologists will have to address the problem of developing quantitative theories of particle size distributions in communities for which size-dependent feeding is not the dominant organizing force.

THE PARTICLE SIZE SPECTRUM

In its simplest terms a particle size spectrum is a histogram describing how many particles fall into each of several different size ranges. Translated into operational terms there are several refinements and complications which arise. The size classes are usually defined so as to be equal on a logarithmic scale, and automated counting systems usually use classes which increase by a factor of two in volume or mass (Sheldon and Parsons 1967). There are generally many more particles in the smaller size classes than there are in the larger ones, so total volume or biomass is a more convenient variable than number. The definition of the size of a particle is a difficult question which must often be settled in a less than satisfactory way by operational considerations such as the idiosyncrasies of the measuring apparatus; for living particles the appropriate measure might be dry weight or surface area (Harding 1977, Brodie 1982), but often something less satisfactory like a linear dimension is used. The issue, although important, is not necessarily of fundamental concern, since they are all highly correlated; however, the use of a convenient proxy measurement like wet weight to describe the energy content of an organism is bound to increase the scatter of the data around any model which is basically correct (Cammen 1980).

Given all of these difficulties, it is indeed surprising to find that particle size distributions are quite regular. The most general and striking characteristic of many of the marine distributions is that the total biomass in logarithmically equal size intervals is roughly comparable, even though the size range covered is enormous (from a few micrometers to several dozen meters in length, meaning a factor of more than 10^{20} in mass or volume, and a correspondingly great factor in the number of particles). This is one of several patterns which are characteristic of different environments; pelagic distributions tend to be smoothest, while coastal distributions have a regular pattern of bumps, and benthic distributions have two very pronounced and characteristic minima. Thus there are basically two types of theoretical questions to be dealt with; one is to understand the basic regularity, and the other is to understand how these different patterns arise.

BIOENERGETIC MODELS

Theoretical work so far has focussed on explaining the regularity of pelagic distributions, using conservation of energy as the underlying assumption. Kerr (1974) developed the first equilibrium model for a size-structured food chain, while Platt and Denman (1977, 1978) looked at the steady state formulation of a continuous model incorporating growth and respiration. The Platt-Denman model was developed into a dynamic model by Silvert and Platt (1978), and in a later form of the model they incorporated spatial heterogeneity and some degree of taxonomic disaggregation (Silvert and Platt 1980).

The Silvert-Platt model is basically in the form of a von Foerster equation, which in turn is based on the flow equations of hydrodynamics; the difference is in the way in which biomass or energy is transferred from one part of the size spectrum to another. Whereas hydrodynamic flows are basically continuous, in that a molecule of fluid cannot get from one place to another without following a continuous trajectory between them, this is not true in the modelling of size distributions. One can treat size as a fourth dimension, and whereas flows due to normal growth are continuous (i.e., when an organism grows from one size to another it passes through all intermediate sizes), the same is not true of energy transfers due to predation or reproduction, or indeed to growth involving metamorphosis. Furthermore, some of these processes, predation for example, are nonlinear and thus introduce a major mathematical complication. It appears that these nonlinearities may destabilize the system and be responsible for the strength of the seasonal cycles which are observed in temperate marine ecosystems (Silvert and Platt 1980).

The basic form of the continuous equations is:

$$D\beta/Dt+\mu\beta=S$$

where β is the biomass density as a function of size w and the position vector, μ is a loss term incorporating respiration and non-grazing mortality, and the four-dimensional flow derivative D/Dt is defined by

$$D\beta/Dt=\partial\beta/\partial t+\partial(\beta g)/\partial w+div(\beta v)$$

where g=dw/dt is growth. The source term S incorporates discontinuous flows such as the transfer of energy from large particles to the smaller sizes by reproduction, and the transfers due to predation which usually go from smaller organisms to larger ones in aquatic systems. Growth plays the role of velocity in the fourth (size) dimension in this formulation; however, the situation is complicated by the essential nonlinearities introduced by predation, since not only are the sources and sinks on the right-hand of the equation affected by this, but also the growth rate g depends on ingestion.

A serious difficulty associated with the existence of flows which are discontinuous in the size "dimension" is that boundary conditions must be specified over an interval, rather than simply at the boundary of the region. In biological terms this means that for a continuous model, such as the original Silvert-Platt (1978) formulation, the phytoplankton are represented by particles of a single size which drive the entire system, but in the later approach an entire size spectrum of primary production must be specified (Silvert and Platt 1980).

Because of these mathematical difficulties, detailed solutions of the model equations have not yet been carried out. Before doing so it seems essential to ensure that all aspects of the model formulation are correct, and there are grounds for believing that the predation submodel used may not be realistic. Silvert and Platt (1980) used the quadratic interaction characteristic of Lotka-Volterra models, but when the size range of particles grazed by a given size of predator is large this may lead to spurious instabilities of the type associated with omnivory in Lotka-Volterra food web models (Silvert 1982). This can be avoided by using more realistic submodels, such as one based on size-selective feeding (Silvert, in preparation).

THE ROLE OF DIMENSIONALITY

The bioenergetic approach, although satisfactory for the study of pelagic ecosystems, does not seem to be justified in physically structured environments such as those associated with benthic communities. The regularity of the distributions found for these communities (Schwinghamer 1981) suggests that conservation of energy is only one of the factors affecting the underlying size structure of ecosystems (Smith 1976). The existence of a general typology for size structures in different environments indicates that there may be a fundamental link between these environments and the kinds of particle size distributions they can support, regardless of the evolutionary history of the particular region.

An obvious feature which distinguishes pelagic communities from benthic or terrestrial ones is dimensionality, in that pelagic marine organisms live in an essentially three-dimensional environment, while terrestrial organisms are restricted to two dimensions and soft bottom benthic environments seem to fall somewhere in between. While this idea requires further quantification (dimensionality is not normally considered a continuous variable, even though the use of fractional dimensions has proved useful in the study of phase transitions), some of the ways in which dimensionality affects size structure are quite clear. The existence of a two-dimensional substrate is essential for the growth of macrophytes, and thus pelagic marine ecosystems are distinguished by the fact that primary production is restricted to unicellular algae. Because of physiological constraints on feeding behaviour this means that herbivores must also be small, which leads to the close connection between size and trophic level which must be an important contributing factor to the relatively uniform size distributions found in these systems. Another contributing factor is the fact that in water the speed of a swimming organism is closely related to its size, so that larger predators can chase their prey more rapidly. However, there is no significant dependence of speed on size in the terrestrial environment (Gunther and Morgado 1982), so frequently predators are smaller than their prey. Dimensionality and the importance of gravity on land also play a role here, since a small active raptor often catches prey by crippling it and bringing it down, while in the water the predator more often needs to engulf the prey completely to capture it. Furthermore, terrestrial raptors often operate in groups and surround prey, which is practical in two dimensions but is virtually impossible in three.

Since primary production on land is mainly by macrophytes, the size of herbivores is not constrained in the same way as in the water. A more important factor appears to be seasonal changes in plant biomass which make mobility essential. Herbivores tend to be much more mobile on land than in the water, even though the range of sizes (from small insects to elephants) is very great. Thus we find that primary production consists of macrophytes ranging in size from grasses to trees, but the herbivores almost always include large vertebrates such as ruminants, and the carnivores are of an intermediate size.

The smaller terrestrial animals, notably insects, may have an airborne phase, and thus they occupy an environment of dimensionality intermediate between land and water. This may be why the marine pattern of larger eating smaller is more prevalent among this group, since the capture process and dependence of speed on size among flying carnivores is similar to that found in the sea. Similar remarks may apply to animals which live within the soil.

Another aspect of dimensionality is that it is easier to search on a plane than in three dimensions, and thus spatial dispersion plays a different role in the two environments. This may also be important in determining the size structure of predators, since a small randomly searching predator has a better chance finding prey in two dimensions than in three.

The benthic community is intermediate in many respects, particularly since some macrobenthic organisms have pelagic phases. There are a number of factors which make the benthic environment unique. Predator-prey size ratios are not as regular as they tend to be in other environments, and often this is directly related to the nature of the substrate; deposit feeders, for example, can scrape diatoms and bacteria off the surface of sand grains in a way which permits even large benthic grazers to feed on these microscopic organisms. It is likely that studies of size structure in benthic communities will play a major role in

helping us understand the relative importance of a two-dimensional substrate in a three-dimensional living universe.

DISCUSSION

The above arguments are highly speculative, since it is one thing to show that we can build plausible models of particle size distributions in different types of ecosystems but quite another to demonstrate that these models lead to fundamental insights about how these different ecosystems are organized. Certainly the existence and nature of a substrate is a major determinant of ecosystem organization, and Marcotte (1977) has pointed out that dimensional differences in the feeding environment are an important factor in niche differentiation. Particle size distributions are likely to prove the best way to investigate such questions, since a highly aggregated description seems most appropriate for a problem of this degree of generality, and studies of system aggregation have shown that aggregation by body size, which is basically the same as aggregation by turnover time (Humphreys 1979, Banse and Mosher 1980), is usually superior to other approaches (Cale and Odell 1979, O'Neill and Rust 1979). The use of allometric relations to estimate physiological rates for system models of this type makes it possible to use particle size distributions for different kinds of ecological investigations (Platt and Silvert 1981), so models of this type can be quite general despite the simplified level of system description. Particle size distributions have proven useful in the the study of bioenergetic flows in pelagic ecosystems, and they may well prove of even greater value in the study of more general and perhaps fundamental questions in ecology.

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