

### 2.2.3 MODELS OF PARTICLE-SIZE SPECTRA<sup>1</sup>

#### *Introduction*

Until the middle of the last decade the description of the structure of ecological communities was usually accomplished by grouping organisms according to taxa or trophic level. Compartmental contents and flows between aggregations were described in terms of mass or energy. One of the challenges of experimental community ecology has been the total quantitative description of the contents of and exchanges between compartments. Complete taxonomic identification within a community is difficult, not to mention the herculean task of quantifying all exchanges between the species. The aggregation of species into trophic levels, likewise, has been wrought with ambiguities (Hutchinson, 1959). Any alternative which would allow rapid and repetitive measurement of ecosystem structure would, therefore, hold high potential for

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accelerating the progress of ecosystems research by increasing the rate of data acquisition.

A priori there is no reason to aggregate organisms only by taxa or trophic level. Grouping individuals by size, age, or metabolic level might lead to a more accessible interpretation of ecosystem structure and dynamics. In fact, descriptions of particle-size distributions (psd's) in seawater have been made microscopically (Riley, 1963), by filtration (Mullin, 1965), and by light scattering and transmission techniques (Jerlov, 1961). But none of these techniques combined the speed and accuracy inherent in the electrical measurement of the number and volume of particles passing through an orifice. This methodology had proved so useful in biomedical research that by the mid sixties a commercial unit (the Coulter Counter) was on the market, and Sheldon and Parsons (1967) were using the tool to examine psd's in seawater. More recent advances in particle-size measurement, e.g. by means of acoustics and laser holography, have extended the range of particle sizes which may be counted automatically (see Parsons and Seki, 1969, and SCOR, 1973).

In the new perspective afforded by rapid particle counts, plants, animals, detritus, and inorganic material are integrated into compartments characterized by size alone. The key concern of this section is how the structure of particle-size distributions in pelagic ecosystems can assist in the description of community dynamics.

#### *Early empirical work*

One of the first problems in applying the new particle-counting technology to ecology was how best to present the data for subsequent analysis. The data are most easily read from the apparatus as the number of particles of a specific volume. Since very small particles tend to dominate in numbers, most graphs of counts versus volume look much the same, having a peak at the low end of the spectrum and quickly decaying to relatively minuscule counts at higher sizes.

But the smaller number of larger particles could occupy a greater proportion of the total sample volume than their numbers would indicate. Multiplying the numbers by the individual particle volume gives the total volume of particles in that size class. Normalizing this product with the total volume of water examined gives the volume concentration of particles of a given size class (usually expressed in ppm). The plot of the volume concentration versus the logarithm (in octaves) of the particle diameter has, therefore, become the standard way of representing particle-size data.

Sheldon and Parsons show how a bloom of the diatom *Skeletonema costatum* (c. 40  $\mu$ ) becomes strikingly apparent when graphed in the above manner, in spite of being invisible on a plot of particle counts versus particle diameter.

With methodological questions settled, the application of particle-size data to ecological research could begin. Parsons (1969) perceived psd's as

enabling the rapid determination of the diversity of pelagic ecosystems. By dividing the total particle volume in size class  $i$ , by the volume of all particles, one arrives at the probability,  $p_i$ , that an atom of biomass will be included in a particle of size  $i$ . The community size diversity is thereby described as

$$D = -\sum_i p_i \log p_i, \quad (66)$$

and may be regarded in the same way as species number or species biomass diversities. The inability, however, of ecological research to establish a firm relationship between diversity and stability caused interest in diversity indices to wane, and Parson's index does not appear to have engendered much subsequent enthusiasm.

Since psd's could be quickly obtained, it became possible to search for a pattern in the large number of size spectra from various marine pelagic communities. Sheldon *et al.* (1972), therefore, collected over a hundred psd's in the 1–100  $\mu$  range from the surface waters of the Atlantic, Pacific, and Southern Oceans and from deep waters of the North Atlantic, South Pacific, and Southern Oceans. Indeed, surface-water spectra did appear to fall into four distinct groups characteristic of the polar, temperate, subtropical, and equatorial regions. The most ubiquitous pattern, however, was no pattern at all, i.e. a uniform distribution of particle concentration over all size classes measured. Uniform particle concentrations dominated the subtropical surface waters and the deep water samples at all latitudes.

Sheldon *et al.* discussed the possibility that uniform concentration distributions might be extrapolated beyond the size ranges studied. Estimates of standing stocks of larger organisms such as zooplankton, micronekton, and whales showed that, while concentrations might fall off slightly for larger-sized organisms, the drop is less than a factor of five over seven orders of magnitude in size. Thus, a uniform distribution over all size classes provides a convenient rule of thumb for estimating the abundance of animals when only their size is known (Sheldon and Kerr, 1972).

Furthermore, there are ecological implications behind the observations of uniform size concentrations. The pelagic food chain relationships in the ocean are generally such that relatively large predators feed on relatively small prey. Therefore, uniform concentrations at all sizes can only be maintained if the rate of particle production varies inversely with particle size. The authors assembled half-life data from organisms spanning six orders of magnitude in size to show that a tight correlation does exist between doubling time and size.

#### *Modelling Sheldon's hypothesis*

Any empirical observation, such as Sheldon's sweeping hypothesis of uniform size concentrations, immediately begs for more formal description. How does the empirical fact relate to observations on the size dependency of other physiological factors, such as metabolism? Kerr (1974a) attempted a synthesis

of observations on psd's, growth rates and metabolic rates by invoking an energy budget after Winberg (1960). Doubling time was assumed to be a power function of organism size

$$\tau = aW^b, \quad (67)$$

where  $\tau$  is the doubling time,  $W$  is the weight (size) of an organism, and  $a$  and  $b$  are numerical constants. Similarly, metabolism was described by the formula

$$T = \alpha W^\gamma, \quad (68)$$

where  $T$  is the metabolic rate and  $\alpha$  and  $\gamma$  are numerical constants. Coupling these descriptions with the assumption that predators only devour prey whose weight fraction is a constant fraction of their own, Kerr showed that the ratio of volume concentrations between successive trophic levels varied as the predator weight to the  $\gamma + b - 1$  power. Whence, Sheldon's hypothesis of uniform volume concentration requires that  $\gamma \approx 1 - b$ , that is, the rates of growth and metabolism of various organisms respond similarly, on the average, to changes in body size.

Of course, it remains a logical impossibility that volume concentrations remain constant for arbitrarily large organisms (Bader, 1970). Any real collection of particles must have a maximum particle size (even the collection of all the organisms in the ocean). Furthermore, Sheldon *et al.*'s extrapolation to very large sizes showed a slight downward trend, which the authors preferred to dismiss as the underestimation of stocks of large-sized species. Platt and Denman (1977) combined an alternate analysis of energy flow up the food chain with Fenchel's (1974) values for the power law constants in Equation (67) and Equation (68) to show that the volume concentration of particles should decline roughly as the negative one-fifth power of body size. Interestingly enough, Platt and Denman (1978) found that the decline in particle concentrations could be explained almost entirely by losses to metabolic respiration. Losses to the detritus food chain through an assimilated ration have a negligible effect on the predicted psd.

The insight gained by the steady-state analyses prompted attempts to generalize the psd models. With no further assumptions Silvert and Platt (1978) were able to extend Platt and Denman's analysis into a description of transients in a psd. The assumption that losses from a given size category are proportional to the biomass of that compartment guarantees that the first-order partial differential equation describing the psd may be solved analytically. The solution specifies that any transient in the system will propagate up the spectrum without change in shape. If the transient has the form of a pulse disturbance, the relative heights of the peak at two different times will be in the same ratio as the steady-state values. There is no diffusion of the peak as it evolves. One may imagine a snake swallowing a rabbit—the lump of prey can be seen travelling intact down the body, maintaining its shape while diminishing slightly in size during the passage.

Intuitively one would expect pulse disturbance in a psd to spread as it

moves to larger sizes. Also, one would expect some 'feedback' of the pulse to smaller-sized particles. That the time-dependent model of Silvert and Platt failed to predict such behaviour prompted the investigators (Silvert and Platt, 1980) to seek a more inclusive form of the time-dependent equation for psd's. The derivation begins with the equations of detailed balance of biomass among the size compartments

$$\frac{db_i}{dt} = S_i = \sum_j (f_{ij} - f_{ji}), \quad (69)$$

where  $S_i$  is the net rate at which material flows into compartment  $i$  and is expressed in terms of the transfer rates  $f_{ij}$ , which represent flows into compartment  $i$  from compartment  $j$ . The contributions to the  $f_{ij}$  due to reproduction, predation, growth, advection, and diffusion are described in turn, until the master equation takes on a form similar to the equation of species continuity in a fluid flow field—the primary difference being that Silvert and Platt's formulation has particle-size concentration as the dependent variable.

As the master equations form a coupled set of non-linear partial differential equations, a general analytical solution is impossible. Silvert and Platt do, however, solve a limiting form of the master equation for a homogeneous system in which predation (represented in a quadratic fashion) is the dominant biological flow term. The feedback due to predation is in the direction of increasing size, and a step-function increase at small autotrophic sizes is likely to lead to a further increase in small-particle concentration because of reduced grazing pressure. The result is a wave-like instability that may take a long time to die out.

If Silvert and Platt seemed reluctant to forego analytical methods in favour of numerical simulation of the coupled non-linear master equations, Steele and Frost (1977) were not. They derived a model for nutrient-producer-herbivore-carnivore interactions in a pelagic ecosystem. The size of the producers and the length of the herbivores were the only two dependent variables for all processes. Simulations of the model indicated that size structure can be at least as important, and probably more significant, than the total biomass of a population to understanding the exchange of energy between trophic levels. Steele and Frost's model can be viewed as a particular case of the master equations of Silvert and Platt.

#### *Other empirical efforts*

It is useful to note that all of the previously described modelling and theoretical efforts can be traced back to the Sheldon hypothesis of uniform volume concentration. This hypothesis, in turn, was based on psd's taken at 100 stations around the world's oceans with fewer than ten distributions from various depths at selected stations. While this is an impressive data base for a single project, it soon becomes apparent that theoretical exercises are extending well beyond their data base. Further development of concepts regarding psd's is

likely to be slowed by a dearth of well-planned experiments centred about the measurement of particle size.

Although Sheldon *et al.*'s observation on uniform particle concentrations has received much subsequent attention, it constituted only half of their reported discussions. As mentioned, they also described psd's characteristic of four major oceanic zones. What Sheldon *et al.* did qualitatively can also be accomplished in a more quantitative manner.

For example, Kitchen *et al.* (1975) employed principal-component analysis to describe particle spectra taken off the Oregon coast during the summer. The first two principal vectors accounted for 92 per cent of the intersample variance. When each sample was plotted according to its weighting factors for the two principal vectors, the samples could be segregated into three separate groups according to whether the sample came from the clear deep waters, the high-salinity surface waters, or the low-salinity surface waters.

Chanut *et al.* (1977) performed much the same analysis on spectra from the Gulf of St Lawrence Estuary and identified five separate regions of the estuary. During a subsequent survey, whenever spectra approximating either of two specified psd's occurred, twenty-one other variables characterizing biotic and abiotic materials were also measured. The twenty-one variables were themselves differentiated using principal-component analysis, and the patterns of association of the biochemical parameters with respect to the principal axes differed markedly in the two regions. In the first (upstream) region terrigenous matter associated strongly with the principal characteristic vector, whereas the downstream segregation showed a greater association of biological variables with the primary vector. Thus, the authors were able to characterize the particles according to probable origin.

#### *PSD's and holistic ecology*

Having reviewed the theoretical and empirical work on psd's, one might rightfully ask how these endeavours help to define a holistic approach to ecosystems analysis. While it is true that a certain degree of aggregation is accomplished in lumping particles according to size, it is not immediately clear how a particle-size distribution culminates in a single community variable or a small set of variables which characterize the structure of the entire ecosystem. It is true that Parsons was tending towards a holistic description of community particle-size structure when he assigned diversity indices to psd's. But particle-size diversity, like its taxonomic counterpart, is a measure based on compartment content and is likely to be of little assistance in elucidating systems dynamics.

Perhaps this last statement requires further explanation. Today it is trite to say that an ecosystem consists of its component species and their interactions. But it is not as widely perceived that if one wishes to describe the behaviour of a community, one should give priority to determining the interactions among compartments over assessing the contents of the compartments themselves.

Translated into more practical terms, if mass or energy is the currency in an ecosystem, a primary goal should be the determination of the *flows* of mass or energy—a goal which is at least as important as a description of the mass or energy content of the compartments. Specific examples of relevant flux measurements are rates of excretion, production, respiration, feeding, physical transport and so on. A holistic description of community flow structure appears more likely to be of value in explaining ecosystem development than a description of compartmental contents.

This may indicate why species diversity, a community measure based on content, could not characterize the dynamic notion of stability. In contrast, Mulholland's (1975) rigorous application of information theory to energy flows yields community variables useful in hypothesizing a coherent theory of organization in ecosystems encompassing the notions of self-organization, complexity, redundancy, and stability (Ulanowicz, 1979b).

Now particle-size distributions are measures of compartmental content. It is unlikely that a single determination of particle-concentration distribution will say much about the community dynamics of the pelagic ecosystem. In fact the insights provided by the models described in this section actually come about by balancing flows through the chain of compartments—the steady-state psd simply serves as an empirical constraint on the balance. Any effort to generalize the results will invariably lead to what Silvert and Platt aptly term the 'master equations', i.e. the balance of flows among the compartments as described by Equation (69).

Unfortunately, one cannot unambiguously infer the flow structure among size compartments by observing solitary psd's. One can, however, gain considerable information about the flow structure by collecting a time series of psd's at a given location.

#### *Implications for design of research programmes*

One is inclined to propose an observational programme along the following lines. Particle-size distributions are measured in a pelagic ecosystem at regular intervals. The length of the interval between determinations would ideally be less than the turnover time of the smallest organisms that will be measured (as estimated from Equation (67)). The duration of the series ideally should be greater than the turnover time of the largest organism in the distribution. In addition to particle size, other convenient variables such as temperature, salinity, and water velocity should be determined at each sampling time. Ideally, one would also hope to measure certain descriptive biochemical parameters such as nutrients, chlorophyll, lipids, and ATP according to the same sampling protocol.

If the particle-counter records over  $n$  channels and  $p$  additional factors are monitored, one has  $n + p$  separate time series. Cross-correlation of the rates of change of the  $n$  size channels should yield clues on intercompartmental transfers. Correlation between the particle sizes and the descriptive parameters

should provide hints as to the qualitative nature of the flows. Fourier time spectra for each of the  $n$  channels may reveal the frequencies in the environment to which each size class is attuned.

Such an endeavour should produce a host of hypotheses concerning possible mesoscopic (intercompartmental) flow mechanisms. What is perhaps more important, it may offer an acceptable method for estimating a measure of the dynamic structure of the community. Assuming that the percentage of the total system variance attributable to channel  $i$  is  $V_i$  over the period of observation, and calling the partial correlation coefficient of size class  $i$  with any other channel  $j$ ,  $r_{ij}$ , then the average mutual information among the  $n$  channels becomes

$$I = \sum_{k=1}^n \sum_{j=1}^n r_{kj}^2 V_k \ln \left[ r_{kj}^2 / \sum_{i=1}^n r_{ij}^2 V_i \right]. \quad (70)$$

This measure is less fundamental than Mulholland's (1975) analogue based on energy flows, but, unlike Parson's diversity index, it is descriptive of the dynamics of the system. Since organisms are lumped according to a controllable number of size classes, there is greater opportunity to compare the indices of two different pelagic ecosystems—regardless of their taxonomic constitution. Furthermore, if one is willing to assume that a greater index of dynamic structure implies increased capability for self-organization, one may order various ecosystems according to their stage of development. Conversely, a decrease in the value of dynamic structure would likely signify a breakdown of the system in the face of inordinate stress.

The automatic measurement of particle-size distributions in marine waters provides several advantages in the analysis of pelagic ecosystems. Unlike taxonomic descriptions, the format of the data is uniform and controllable, i.e. two very different ecosystems may be compared by using the same size-range and number of channels. A virtually synoptic picture of the entire ecosystem can be obtained with relative ease and accuracy. The range of sizes over which measurements can be made is expanding (Pugh, 1978).

Whenever possible psd's should be taken along with other data on pelagic ecosystems. Single psd's have little value in elucidating ecosystem dynamics, however, implying that consideration should be given to collecting temporal series of psd's.