

ZOOPLANKTON PATCHINESS

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Introduction

In the early days of research on lake plankton it was generally assumed that the zooplankton was distributed more or less homogeneously in the horizontal plane. In recent years, however, it has been recognized that zooplankton populations are highly aggregated in the horizontal as well as the vertical plane. Zooplankton patches can be detected on scales ranging from centimetres to kilometres, and it is now known that many physical, chemical and biological factors are involved in the formation and dissolution of these patches. Much of my work at the FBA and elsewhere has centred on the problems of sampling and analysing this transient, highly mobile, organization.

This review considers three general aspects of research on zooplankton patchiness: the detection of patchiness, the description of patchiness and the causes of patchiness. Early studies of patchiness (e.g. Ricker 1937) were largely preoccupied with the statistical problems of proving departures from randomness. Later studies (e.g. Colebrook 1960a) placed more emphasis on defining the spatial scales of patchiness and relating these patterns to structure in the physical environment.

The detection of patchiness

The distribution of a population in space reflects the total interaction between the population and its environment (Taylor 1970). Although the spatial distribution of a species may be a real characteristic, the detection

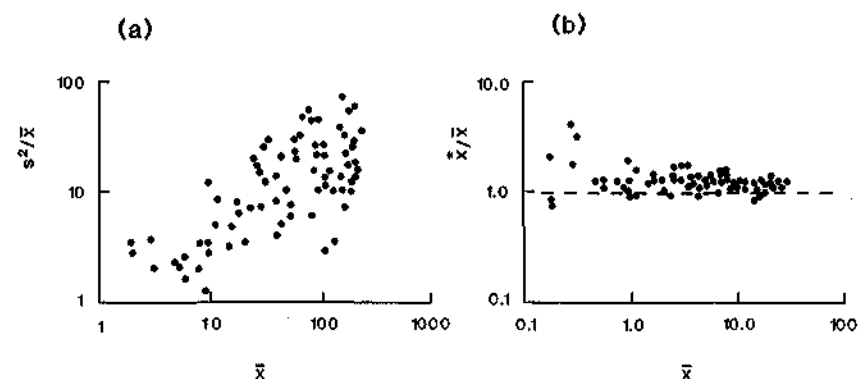


FIG. 1. The relationship between two indices of dispersion and population density: (a) the variance to mean ratio; (b) Lloyd's measure of patchiness. Both indices for *Daphnia hyalina* in Eglwys Nynydd reservoir (1971). Modified from George (1974).

and measurement of non-randomness in a set of samples is usually dependent on the size, and sometimes even the shape, of the sampling units taken (see Elliott 1977). For many years, Fisher's coefficient of dispersion (the ratio of sample variance (s^2) to sample mean (\bar{x})), was used by plankton ecologists, both as a means of detecting patchiness and as a measure of the degree of patchiness. Many concluded that their populations were randomly distributed when the real problem was their inability to detect non-randomness. Quite often their sampling units contained too few individuals for tests on the variance/mean ratio to disprove randomness. Agreement with a Poisson series is the accepted test for randomness (see Elliott 1977). The variance/mean ratio is a good statistical test for agreement with a Poisson series, but is an exhaustive test for departures from randomness only if the sample is large and a range of sampling-unit sizes is selected. When the distribution of a population is truly random, the variance increases steadily with sampling-unit size and the variance/mean ratio is always near unity.

When it becomes necessary to quantify different patterns of dispersion in populations, indices based on the variance/mean ratio are usually inappropriate since they are nearly all influenced by the number of individuals in the sample. For example, Fig. 1(a) shows the tendency for the variance/mean ratio to increase with an increase in population density in samples of *Daphnia* from a shallow reservoir. The reciprocal of k in the negative binomial is often used as a more appropriate index of dispersion when low- and high-density populations are being compared. Although this index is relatively independent of population density, its application strictly implies agreement with a particular frequency distribution model (the negative binomial). A more generally acceptable measure of patchiness is that based on the index of 'mean crowding' (Lloyd 1967). The sample estimate of mean crowding (\hat{x}) is given by:

$$\hat{x} = \bar{x} + \left(\frac{s^2}{\bar{x}} - 1\right)$$

The ratio of mean crowding (\hat{x}) to mean density (\bar{x}) is then a suitable measure of patchiness. I used this index to analyse the dispersion patterns of zooplankton in a eutrophic reservoir (George 1974). The index equals unity for a random distribution, is less than unity for a regular distribution and is greater than unity for an aggregated distribution. Like $1/k$ this measure of patchiness is relatively independent of population density (Fig. 1b), and has the added advantage of remaining positive for all patterns of distribution as long as $x > 1$. Unfortunately confidence limits for individual estimates of patchiness can be calculated only where large samples are collected or it is possible to make some assumptions about the nature of the underlying patchy distribution. Where small samples are collected at regular intervals from the same population, regressions of mean crowding on mean density (Iwao 1968) may be used to provide additional information on

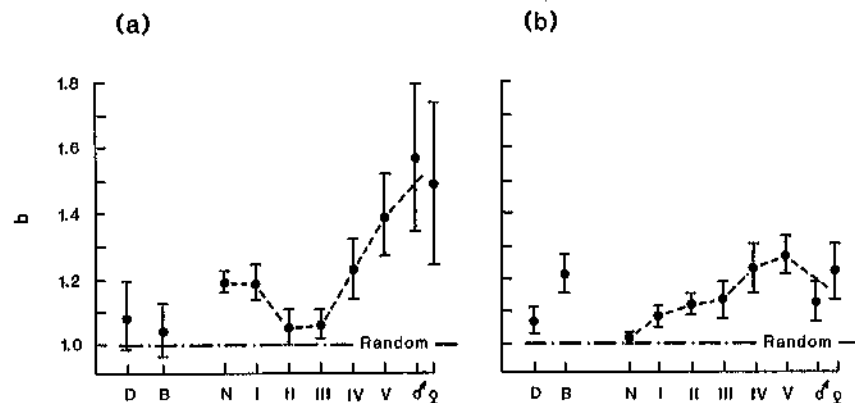


FIG. 2. Graphical comparison of slope coefficients (b) for regressions of mean crowding (\bar{x}) on mean density (\bar{x}). The value of b is an index of spatial pattern where $b > 1$ indicates a patchy distribution. Data from Eglwys Nynydd reservoir in (a) 1970 (b) 1971. D = *Daphnia hyalina*; B = *Bosmina longirostris*; ♀ = *Cyclops vicinus* adult females; ♂ = *C. vicinus* adult males; Roman numerals = *C. vicinus* copepodite stages; N = *C. vicinus* nauplii. Modified from George (1974).

spatial pattern. I applied such methods to the analysis of zooplankton patchiness in the reservoir (George 1974) and found that different species and life-stages showed characteristic patterns of distribution. A comparison of slope coefficients for the mean crowding/mean density regressions, for example, showed a tendency for patchiness to increase from instar to instar in the *Cyclops vicinus* population (Fig. 2). These differences almost certainly reflected the animals' increasing capacity for directed movement as they grew through their developmental stages.

The description of patchiness

One approach to the description of spatial pattern is to collect a large number of random samples from a population and then decide which of the many probability distributions gives the best fit to the data. In addition to the basic binomial family of distributions (Poisson, and Positive and Negative Binomial), a number of other mathematical models have been developed to describe various non-random distributions e.g. that of Anscombe (1950). The 'goodness of fit' of the observed distribution to these fundamental models has, in the past, been used to define structures of real biological significance. In recent years, however, it has been recognized that the same distribution can often be generated by different and even contradictory hypotheses. A given species may show different distributions within the same habitat at successive intervals of time, or even at the same time in different areas.

In the open-water environment, gradients are very important in determining the structure of plankton organization. Any sampling scheme designed to analyse spatial pattern must therefore take into account the spatial disposition of sampling units and ideally cover a wide range of spatial scales. Much of our recent understanding of spatial variability in the plankton has been gained by the analysis of sequential samples collected at regular intervals along fixed transects. In 1970 and 1971 I used a simple pumping system that collected samples over small horizontal distances to examine the dynamics of zooplankton patch formation and dissolution in a eutrophic reservoir (George 1972). Most species and life-stages showed small-scale variations in abundance (Fig. 3a) superimposed on any large-scale systematic variations present (Fig. 3b). To understand the complex interactions of factors that produce such patterns, physical and chemical variables must be monitored in parallel with zooplankton sampling. In 1976 I described a simple deck-mounted pumping system for collecting horizontal plankton samples and recording continuously sampling depth, water temperature, turbidity and *in vivo* chlorophyll. Most of the instruments incorporated in this system were available commercially; individual components required little modification and could easily be dismantled and used for other purposes. The system used a Turner Model III fluorometer to measure horizontal variations in chlorophyll-*a*. The *in vivo* fluorescence method of measuring chlorophyll can be used quite effectively to map the vertical and horizontal distribution of phytoplankton in lakes, provided frequent calibrations are made using traditional chlorophyll extraction procedures (see Heaney 1978).

Techniques for the continuous counting and measurement of zooplankton

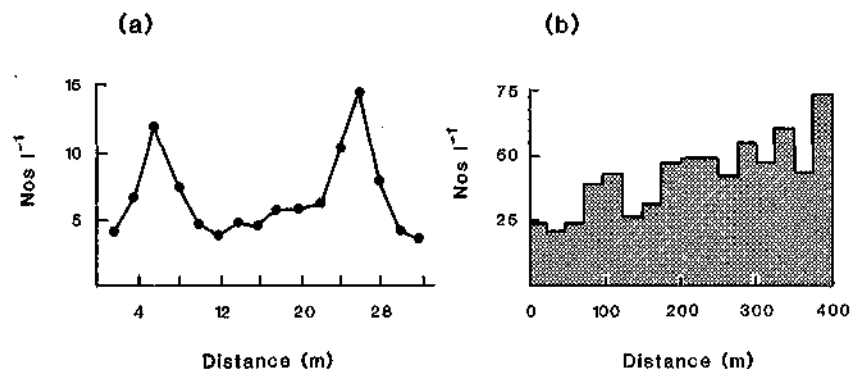


FIG. 3. Small scale (a) and large scale (b) transect samples collected from Eglwys Nynydd reservoir: (a) shows the distribution of *C. vicinus* copepodites in a sheltered bay; (b) shows the distribution of *B. longirostris* along the length of the reservoir. Modified from George (1972).

are still in the developmental stage, but have undergone considerable improvement in recent years (Sameoto & Paulowich 1977). In future the development of more refined sensing techniques such as acoustic holography may even allow us to record the positions of individual animals in the water column (Lovik 1973). Mathematical methods of spectral analysis (Platt & Denman 1975) are now widely used for the analysis of spatial pattern along a transect. In certain circumstances, these techniques go beyond statistical description and provide clues as to the processes underlying the observed distribution patterns.

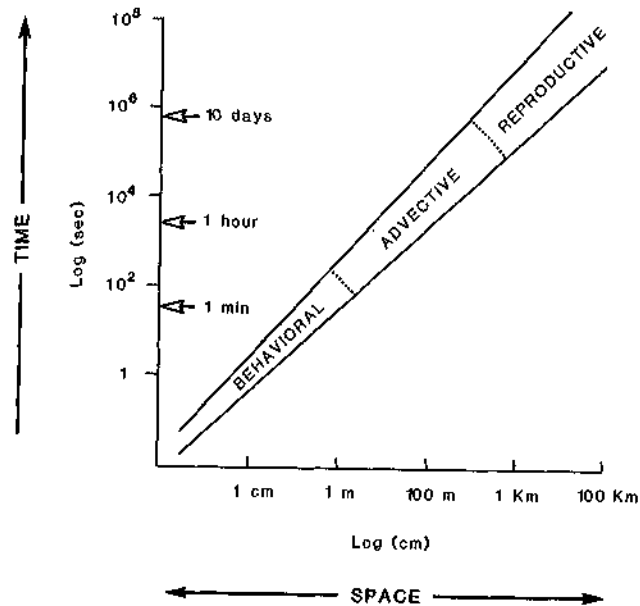


FIG. 4. A very simplified representation of the typical time and space scales associated with different mechanisms of patch formation.

Causes of patchiness

In simple terms, three factors dominate the spectrum of patchiness in most open-water environments:

- (i) Behavioural responses on scales comparable to the 'encounter distances' of individuals. These may include social behaviour within populations of the same species, or predator/prey interactions with other species.
- (ii) Advective (i.e. horizontal transport) effects related to wind-induced water movements, including small-scale variations due to convection cells.

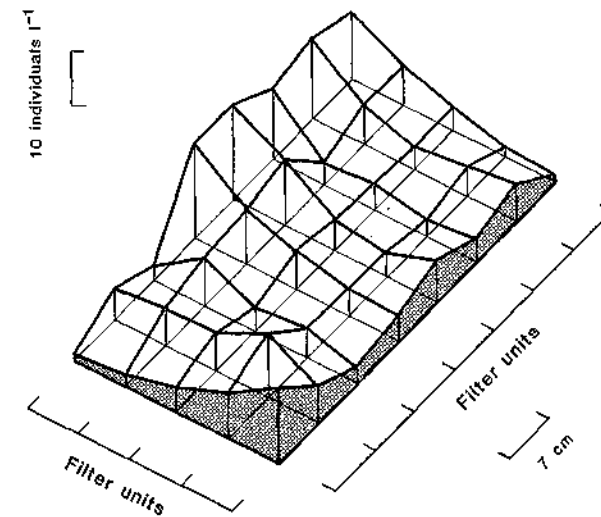


FIG. 5. Diagrammatic representation of the distribution of animals in a small patch of *Daphnia* sampled by the close-interval sampler.

- (iii) Reproductive differences between populations experiencing different food or temperature regimes.

Fig. 4 is a simplified representation of the typical time and space scales associated with these three interrelated factors. In most lakes advective effects play the dominant role; social interactions tend to be easily disrupted by high turbulence, whilst reproductive differences become significant only in very large lakes or lakes with restricted mixing patterns.

- (i) Behavioural patchiness.

Colebrook (1960b) collected dip-jar samples from swarms of *Daphnia hyalina* and *Diaptomus gracilis* in a sheltered bay in Windermere. The *Daphnia* swarm was seen to be about 1 m in diameter and confined to the top 10 cm of the water column. Scattered patches of animals occurred in the surrounding water but concentrations in the swarm were almost two orders of magnitude greater. The swarm contained a much higher percentage of juveniles than the surrounding water, suggesting that the animals had come together by some kind of purposeful movement.

In 1973 and 1974 I observed similar swarms of *Daphnia* in Esthwaite Water and Blelham Tarn and devised a simple close-interval sampler to examine such micro-distribution patterns in more detail. Fig. 5 shows the horizontal distribution of animals detected by this sampler in a sub-surface accumulation of *Daphnia* in Esthwaite Water on a calm, overcast day. The samples were taken near the edge of an elongate swarm approximately 0.5 m

wide and 1 m long. Tests on the variance-to-mean ratio proved that the animals were highly aggregated on the scale defined by the sampling units (normal variable $d=10.09$). Since there was no obvious physical mechanism operating at this scale (5–50 cm), some behavioural response was almost certainly involved.

(ii) Advective patchiness.

In the open water of lakes, the structure and variability of the physical environment are crucial factors influencing plankton distribution. Local accumulations result from movements of organisms, independently or associated with the movements of water. The development of patchiness in a turbulent system ultimately depends on the ability of planktonic animals to direct their movements within a moving mass of water. Zooplankters have little directed horizontal movement at scales above a few metres, but can regulate their vertical position fairly consistently in response to diel changes in light (Banse 1964). Whenever vertical water-movements tend to carry animals from their preferred depth-range, their swimming response will usually produce local accumulations in zones of upwelling or downwelling

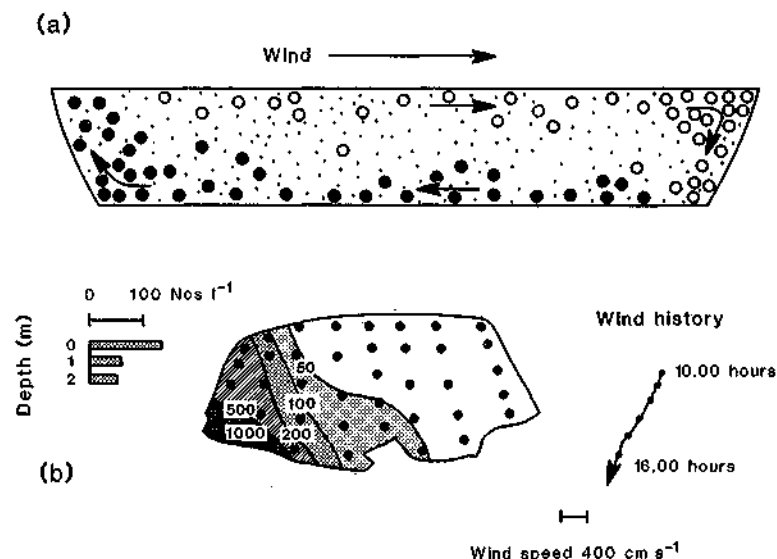


FIG. 6. (a) The 'conveyor-belt' model of zooplankton patchiness: O – animals tending to remain near the surface; ● – animals tending to avoid the surface; ◐ – animals that show no depth selection.

(b) The downwind accumulation of *Bosmina longirostris* in Eglwys Nynydd on 20 July 1971. Vertical distribution shown by bar diagram. Wind history summarized by the progressive vector diagram. Modified from George & Edwards (1976).

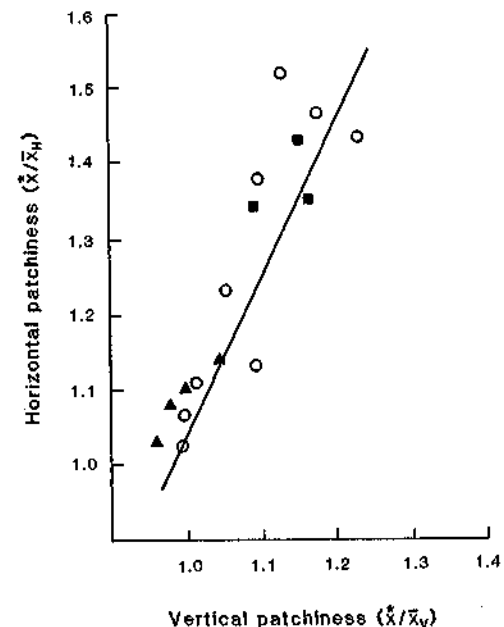


FIG. 7. The relationship between horizontal and vertical patchiness in the zooplankton of Eglwys Nynydd. $y = 0.74 + 1.83x$ ($r = 0.89$). O – *Daphnia hyalina*; ■ – *Cyclops vicinus* copepodites; ▲ – *C. vicinus* nauplii. Modified from George & Edwards (1976).

water. A schematic representation of the development of such aggregations in a 'conveyor-belt' type of wind-induced circulation (George 1981a) is given in Fig. 6a. Animals that make no effort to control their depth distribution remain randomly distributed. Animals having an ascending velocity greater than the descending water velocity become concentrated in regions of downwelling water, whilst animals tending to move away from the surface accumulate in regions of upwelling water.

Local accumulations of zooplankton and motile phytoplankton formed in response to such systematic water movements were demonstrated by George & Edwards (1976) and George & Heaney (1978). An example (Fig. 6b) from George & Edwards (1976) shows local concentrations of *Bosmina longirostris* formed in a shallow reservoir by the downwind transport of animals aggregating near the surface. These accumulations were produced when animals, drifting passively downwind, swam towards the surface in areas of downwelling water. The development of horizontal patchiness under such conditions can usually be related to the development of vertical patchiness by depth selection (Fig. 7). Animals that show less of

a tendency to maintain themselves at a specific depth (e.g. *Cyclops nauplii*) also show little horizontal patchiness.

This simple 'conveyor-belt' model becomes more complex when applied to a large lake such as Windermere, where Coriolis effects (Mortimer 1955) produce very pronounced rotations of the wind-driven currents with depth (George 1981a). Under such circumstances, the horizontal distribution patterns produced by wind-forcing will reflect the relative timing of periods of maximum horizontal displacement and the diurnal vertical migration of the animals. When the lake becomes thermally stratified, the periodic oscillations of the internal seiche may produce even-more-complex patterns related to the animals' response to displacements of the thermocline (Colebrook 1960a).

In addition to the more obvious large-scale directed water movements such as wind-induced currents and seiches, lakes also display a finer structure of turbulence cells with velocities sufficient to influence the micro-distribution of planktonic animals. Langmuir (1938) demonstrated that, under certain conditions, the motions induced by turbulent transport are organized into helical currents in the upper layers of lakes (see Fig. 8b). Convection from this rotational motion generates streaks of foam and debris which are oriented along the wind axis and coincide with lines of surface convergence. Between the streaks are lines of divergence where deep water is carried towards the surface. George & Edwards (1973) used a pumping system to compare plankton density within and between foamlines, and demonstrated that free-swimming *Daphnia* accumulated near the surface mid-way between foamlines (Fig. 8a). Such accumulations of *Daphnia* along lines of divergence almost certainly arise from the tendency of the animals to swim away from the surface on being displaced into a zone of higher light intensity. (Fig. 8b).

(iii) Patchiness produced by population growth.

In very large lakes, or lakes where there are physical constraints on complete horizontal mixing, populations of zooplankton within a water mass may increase in numbers faster than they can be dispersed throughout the lake. There are several theoretical studies relating rates of horizontal diffusion and growth in the phytoplankton (Denman & Platt 1976, Okubo 1978), but little is known of the dynamics of growth-related patches in the zooplankton. Much of the evidence for the existence of such patches in lakes is rather circumstantial. Baldi et al. (1949) found that biometric differences in samples of *Mixodiatomus* collected from Lago Maggiore were related to the distance between samples, and suggested that such differences were due to genetic drift. This seems most unlikely within the space-time scale of Lago Maggiore. The observed biometric divergence could equally well have been produced by the migration of animals from the unsampled hypolimnion. More convincing evidence for horizontal differences in population attributes is presented by Patalas (1969) in his paper on the

horizontal distribution of Crustacea in Lake Ontario. In that very large lake, the horizontal distribution of the zooplankton was primarily related to spatial variations in water temperature and the depth of the epilimnion rather than to wind-induced transport. Whether this effect was produced directly by an acceleration of zooplanktonic growth rates in the warmer water, or indirectly by increased production of food organisms, could not be ascertained.

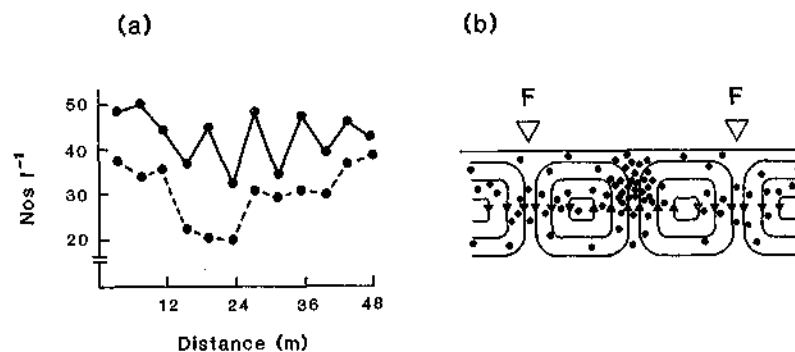


FIG. 8. *Daphnia* distribution within Langmuir circulations: (a) catches of *D. hyalina* within (✓) and midway between (∗) foamlines; (b) schematic representation of zooplankton concentration in an area of upwelling midway between foamlines (F). The plane of illustration cuts through the water surface perpendicular to wind direction. Modified from George & Edwards (1973).

The ecological implications of zooplankton patchiness

This review has briefly outlined concepts of spatial organization necessary to interpret seasonal changes in the zooplankton. The spatial patterns that form in the open water of lakes are in a constant state of change. The transient nature of these distributions nevertheless does not imply a lack of locally deterministic structure. Many apparently stochastic distribution patterns, on closer examination, become explicable in terms of ordered interactions between the swimming behaviour of the animals and their displacement in water currents.

This development of spatial structure in the animal community has wide-ranging implications for the dynamics of the whole open-water system. Spatial patterns may be transmitted both up and down the trophic web, and may even affect the nature of variability in the physical and chemical environment. In June 1974 I sampled zooplankton abundance and the concentration of soluble reactive phosphorus at thirty sites horizontally distributed over the South Basin of Windermere (George 1981b). There was a significant positive correlation between the abundance of zooplankton

and the amount of soluble reactive phosphorus in the water ($r = 0.52$, $p < 0.05$). This result (Fig. 9) suggests that there was a momentary imbalance between the rate of phosphorus excretion and community assimilation rates in the South Basin. Such a situation is most likely to arise when phytoplankton crops are low, zooplankton abundant and the patches subject to little physical disruption. The implications of such small-scale variations in the rate of nutrient regeneration have recently been the subject of much debate in marine plankton ecology (Goldman et al. 1979). In environments where phytoplankton cells encounter patches of nutrients, high transient uptake rates may allow phytoplankton populations to grow at much higher rates than are suggested by the mean nutrient concentration.

The ecological consequences of any patch formation obviously depend on the intensity, size, and persistence of the aggregations. The distance between patches may also be of some importance since this influences the feeding behaviour of grazers and predators. MacArthur & Pianka (1966) have argued that herbivores should be more efficient in large patches. Brock & Riffenburgh (1960) demonstrated theoretically that, for patches to be effective against predators, the distance between patches must be larger than the predator sighting-distance.

Until recently most FBA studies of population changes and lake processes have relied on samples collected at a single station near the middle of the lake. The more detailed studies of seasonal changes upon which we are

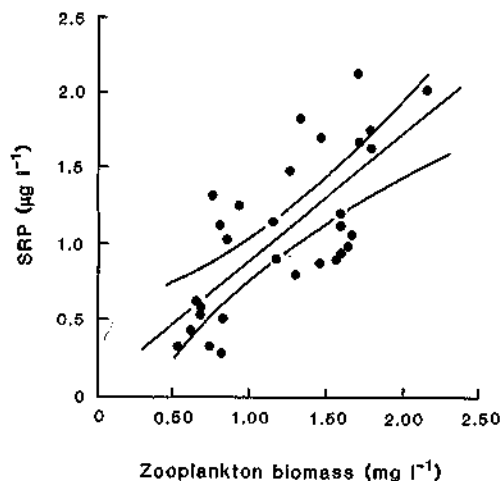


FIG. 9. The relationship between horizontal variations in soluble reactive phosphorus (SRP) and zooplankton biomass in the South Basin of Windermere on 26 June 1974. Regression line and 95% CL indicated ($r = 0.52$). From George (1981b).

now embarking, however, demand more rigorous sampling strategies. In planning such strategies it is important to relate chemical and biological variations in the open water to the physical behaviour of lakes. There is also a need for more detailed studies of the effects of spatial variation on zooplankton population dynamics. The regulation of population size, by density-dependent factors, is a central theme in animal ecology. In most situations, however, we are still unable to quantify the impact of spatial pattern on the basic processes of population change.

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GEOCHEMISTRY OF LIPIDS IN LACUSTRINE SEDIMENTS

P. A. CRANWELL

Introduction

Sediments have been continuously deposited in the lakes of northern Britain since these lakes came into existence at the end of the last glaciation, about 15 000 years ago. The earliest sediments, deposited by the glaciers, are entirely inorganic, but when the ice cover was removed, the land surface was colonized by plants, and organic detritus accumulated in the soil and was transported into the lake by erosion. Aquatic organisms also proliferated and their remains were added to the sediment. This article outlines aspects of research on the organic material found in lacustrine sediments, and the analytical methods involved. Firstly, an explanation of the basic premises of the subject and its terminology is given.

The organic portion of lacustrine sediments, mostly amorphous matter derived from the decomposition of once-living organisms, might appear of little value for recognition of the precursor organisms. At the molecular level, however, many compounds characteristic of the precursor organisms occur in the lipids; these compounds can be separated and identified. The term *lipid* denotes a wide variety of natural products (e.g. fatty acids) readily soluble in organic solvents. Lipids are ubiquitous in living organisms, but the distribution of any given kind of lipid need not be uniform within an organism or over a wide range of organisms. *Organic geochemistry*, the study of organic matter in natural environments, extends the scope of 'natural product' organic chemistry, in which the structure and biosynthesis of constituents occurring in living organisms are studied. The latter field of research has identified compounds that occur only in specific groups of organisms and thus provide *biological markers* to the geological record. The significance of marker compounds in early post-glacial sediments can be better appreciated by a study of present-day events, especially the potential sources of input to contemporary sediments and changes in the microbially-active surface sediment. Such changes, which occur shortly after death of an organism and its burial in unconsolidated sediment, constitute *early diagenesis*.

Sedimentary lipids contain several classes of compounds suitable as biological markers, including alkanes (of general formula 1), methyl ketones (2), alkyl esters (3), alkanols (4), sterols (5), alkanolic acids (6) and hydroxy-alkanoic acids (7) (Fig. 1). Each compound class consists of one or more *homologous series* in which consecutive members differ by one methylene (-CH₂-) group. Within the straight-chain homologous series produced by organisms there is a predominance either of constituents having an odd number (as in alkanes) or an even number of carbon atoms (as in alkanols and alkanolic acids), a feature shown in Figs 3, 4 and 6 by the alternation of