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Spatial Scales of Current Speed and Phytoplankton Biomass Fluctuations in Lake Tahoe

Abstract. *Spectral analysis of current speed and chlorophyll a measurements in Lake Tahoe, California and Nevada, indicates that considerably more variance exists at longer length scales in chlorophyll than in the current speeds. Increasingly, above scales of approximately 100 meters, chlorophyll does not behave as a simple passive contaminant distributed by turbulence, which indicates that biological processes contribute significantly to the observed variance at these large length scales.*

Phytoplankton are small and usually immotile, floating freely in an aquatic habitat. Their growth rates are determined by light, temperature, nutrient concentration, and turbulence—environmental conditions to which they are subjected by physical transport processes. Any spatial patterns of phytoplankton abundance are thus a result of the interactions between transport processes and the differential rates of growth of algal populations under different physical, chemical, and biological conditions. Only limited direct control of physical location can be exercised by algal cells through flagellar locomotion and control of buoyancy.

Theoretical studies of general ecological processes (*1, 2*) and measurements from a variety of habitats (*3*) imply that spatial heterogeneity may be critically important in regulating community and population behavior. Since the epilimnia of lakes are extremely isotropic compared to benthic or terrestrial habitats, and since the organisms are largely unable to control their own location by active means, a demonstration that spatial heterogeneity is important in phytoplankton associations would strongly support the generality of this dimension of ecosystem structure.

Previous workers have sought to account for the complex phytoplankton associations observed even in the well-mixed layer of pelagic systems. Hutchinson (*4*) characterized the existence of multispecific assemblages in such seemingly uniform habitats as the "paradox of the plankton" and proposed that the temporal variability of the physical environment produces diversity. Subsequent investigators have emphasized the importance of spatial heterogeneity in well-mixed turbulent environments (*2, 5, 6*). Phytoplankton populations actually are distributed in nonrandom or patchy fashion on moderate scales (*7*), and theoretical relations between patch persistence, growth rates, intensity of turbulent transports, nutrient uptake rates, and so forth have been investigated (*6, 8*). In situ estimates of phytoplankton biomass can now be obtained by continuous flow fluorometric analysis of chlorophyll concentration, and this permits a direct comparison of the biological and physical structure of pelagic systems (*9*).

During the last 2 years we have made a detailed survey of various physical and biological parameters in Lake Tahoe, California and Nevada, a large (499-km^2), deep (maximum depth, 501 m), extremely oligotrophic lake (*10*) of considerable interest for both basic scientific and management research (*11*). Parameters measured include water currents at three depths, temperature, chlorophyll content, and algal species counts. We present some relations between the spatial spectra of chlorophyll a concentrations measured from a moving boat and the spectra of current fluctuations measured at a stationary meter mounted beneath a subsurface buoy. The spectra show that the direct effects of turbulent diffusion dominate biological processes at relatively small scales (less than approximately 100 m), but that biological processes have greater control of spatial distribution at larger scales.

The interpretation of time series data by power spectrum analysis is common in the physical (*12*) and social (*13*) sciences, but is less familiar to aquatic ecologists (*9*). In considering the spectrum of audible noise, for example, one might wish to know what portion of the sound energy was in a particular frequency band, say 2000 to 4000 hertz. Spectral analysis (*14*) gives a statistically acceptable answer to such questions for stationary time series. In other examples, it might be used to discover how much of the energy in turbulent velocity fluctuations is found at low frequencies (*12*), or how much of the variance in records of a certain economic indicator is due to long-term (low-frequency) fluctuations (*13*).

The chlorophyll data were gathered by pumping lake water from a depth of 18 m through a hose into a fluorometer (G. K. Turner Associates) mounted on a research vessel; the hose assembly was towed behind the vessel at 1.3 m/sec for a distance of approximately 3 km. This in situ method measures both chlorophyll and pheophytin, the concentration of pheophytin in Tahoe having been reported to be about 15 to 25 percent that of chlorophyll a (*15*). During these measurements the phytoplankton association in Lake Tahoe was dominated by a small, nonmotile diatom, *Cyclotella stelligera*. The chlorophyll signal was digitized, stored on magnetic tape, and analyzed for its spectral content with a fast fourier transform algorithm (*16*).

The current meter, a savonius rotor with eight magnetic reed switch pickups, was mounted at a depth of 17 m in Lake Tahoe's well-mixed epilimnion. Each revolution of the turning rotor produces eight pulses, and the time between pulses gives a measure of the low-frequency fluctuations in the magnitude of the horizontal velocity field. The current records discussed here were taken in midafternoon, when daily winds from the southwest of up to 15 m/sec, a standard feature of the Tahoe basin summer climate, drive the surface waters at average speeds of up to 10 to 15 cm/sec. At these speeds we estimate that one can measure fluctuations of the order of 0.5 cm/sec with a length constant of approximately 2 m. The current spectra were also calculated with the fast Fourier transform algorithm.

Since the fluctuations in current speed ($\simeq$1.5 to 2 cm/sec) are small compared to the average speed ($\simeq$10 to 15 cm/sec), the chlorophyll and current records can be spectrally analyzed using Taylor's "frozen turbulence" hypothesis (*17*) and the spectra presented in terms of a wavelength (λ) or wave number ($1/\lambda$). The records discussed here are a current record from 27 September 1973 and a chlorophyll tow from 28 September 1973, although virtually all of our records show the same major characteristics as these. (With time series of chlorophyll concentration and current speed taken at the same time and place correlations and coherence spectra between the records could be analyzed, but other experimental requirements and limits on the data acquisition system did not allow simultaneous measurement.) The thermocline was at 28 m, so both records

were taken from a well-mixed, unstratified portion of the lake with a negligible density gradient, and the effects of internal waves are negligible.

Log-log plots of the current and chlorophyll spectra are shown in Fig. 1. In the region of wave number greater than 10^{-4} cm^{-1} ($\lambda < 100$ m) both spectra show similar linear forms indicating negative power law behavior. The slopes of the linear portions are approximately $-5/3$, Kolmogorov's prediction for the inertial subrange of turbulence (*18*). Both spectra cut off at large wave numbers; at λ less than a few meters a cutoff is expected in the current spectra at the length constant of the savonius rotor (2 m), while the chlorophyll cutoff around 10 m is caused by smearing and small-scale mixing in the hose (inner diameter, 1.6 cm). For $\lambda \geq 100$ m the spectra differ significantly. The chlorophyll spectrum shows a statistically significant peak at 10^{-4} cm^{-1} ($\lambda = 100$ m); this could have resulted from towing obliquely through a pattern of Langmuir spirals (*19*), where phytoplankton were concentrated in downwelling zones, since these regular circulations have vertical scales of tens of meters. For $\lambda > 100$ m the chlorophyll spectrum continues to rise with a steeper slope. The current spectrum shows a break in the interval 1×10^{-4} to 2×10^{-4} cm^{-1} ($\lambda = 50$ to 100 m) and tends to level off at $\lambda > 100$ m. The slopes of the two spectra differ considerably at $\lambda > 100$ m. Leveling off in the spectra of current fluctuations in lakes has previously been observed, although the break appears at different wavelengths (*20*).

We interpret the close resemblance of the current speed and chlorophyll spectra at scales less than 100 m as indicating that turbulence directly governs the distribution of organisms from this region down to the limits of our measurements. Above about 100 m the diverging shapes of the spectra indicate that different processes contribute to the variance of phytoplankton concentration and momentum (*21*). The measurements indicate that above scales of 100 m variations in biological processes such as cell growth, sinking, and grazing have an important effect on the biomass distribution. At these larger scales, spatial heterogeneity of the plankton ecosystem becomes more likely. The existence of a scale length (~100 m) separating one region where a physical process dominates from another where a biological process dominates is in general agreement with theoretical calculations (*6*) and with the observation of variations on kilometer scales in phytoplankton production rates, biomass, and diversity in Lake Tahoe (*22*). The largest-scale variation in phytoplankton is believed to reflect the variation in nutrient content of lake waters caused by stream inflow.

The precise meaning of the observed distribution of chlorophyll in terms of the distribution of populations of organisms and their processes of growth and death remains to be explained. The crucial unknown is the minimum scale at which spatial heterogeneity can result in differential variation in species abundances and hence niche diversity. Phytoplankton enumerations made in conjunction with the work described here have been discussed elsewhere (*23*). The contribution of spatial patterns to the dynamics of population behavior complicates understanding of community processes, perhaps in most habitats. Theories based on conservation laws for energy and momentum lead to simple predictions about the spectral distribution of energy or temperature fluctuations, which are obeyed in a variety of laboratory and geophysical systems (*24*). A similar approach to phytoplankton distributions, based on suitably modified conservation equations, leads to apparently intractable theoretical and field measurement problems because many more processes must be explicitly taken into account (*6*). However, it may be that relatively few of these processes are important. Variable nutrient concentrations from inflowing streams and differential grazing due to zooplankton patchiness are likely to be the most important primary sources of spatial heterogeneity in lacustrine plankton systems. Zooplankton will be important only in moderately eutrophic systems (*25*). The response of phytoplankton populations to the primary sources of heterogeneity is probably a function of two factors: mixing intensity, which is governed by lake size and external weather conditions, and the turnover rate of populations, which affects their ability to respond to ephemeral spatial patterns. Important environmental parameters may be fewer and more easily measured in plankton systems than in most habitats, and the degree of hysteresis may be lower because of the short life spans of phytoplankton. Thus plankton systems may be the best available for examining the role of spatial heterogeneity in ecological processes. Recent advances in algal physiological ecology are the logical complement to the structural studies described here for the empirical description of competition interactions among phytoplankton (*26*).

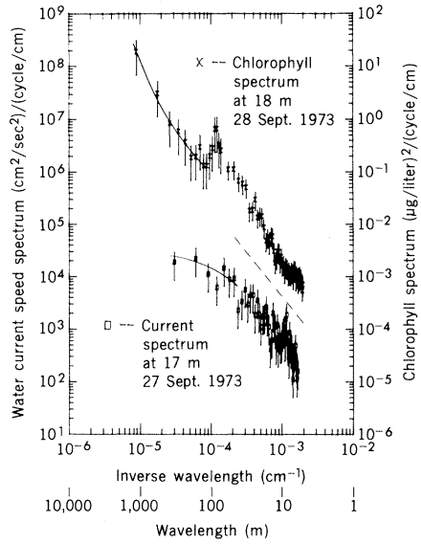

Fig. 1. Log-log plots of the spectra of chlorophyll a variance and current speed fluctuations against inverse wavelength; a wavelength scale is also shown. The error bars indicate 80 percent confidence limits. Both spectra would follow the dashed line with slope $-5/3$ if the current speed fluctuations were in the inertial subrange of turbulence (*18*) and chlorophyll a were a passive contaminant with sources of variance at very large length scales.

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The Possible Role of Histones in the Mechanism of Chromosomal G Banding

Abstract. *Cytochemical data are presented to show that the histone fractions f1 and f2a are involved in the induction of chromosomal G bands, whereas the f2b and f3 fractions are not involved. Removal of the f1 and f2a fractions probably occurs during fixation and is necessary for the induction of G bands.*

During recent years a number of procedures have been devised to induce cross-bands, now known as G bands, of metaphase chromosomes. These procedures include treating fixed metaphase chromosomes with proteolytic enzymes, alkylating agents, protein denaturants, phosphate buffer at high temperature, and many others. The G bands are extremely useful in identification of individual chromosomes and their arrangements, but the mechanism by which G bands are induced remains controversial. It has been suggested that alterations of protein-DNA relationships allow the Giemsa mixture to differentially stain specific regions on the chromosomes (*1–3*). Whether histones or acidic proteins (or both) are involved remains unclear (*1, 2*). We present cytochemical data to show that the histone fractions f1 and f2a are at least partially responsible for the induction of G bands, whereas the f2b and f3 fractions are not involved.

The Chinese hamster fibroblast line Don and the cells of the cactus mouse, *Peromyscus eremicus*, were grown as monolayers in McCoy's 5a medium with 20 percent fetal calf serum. Cells were fixed in Carnoy's mixture (methanol and acetic acid, 3 : 1), placed on slides by the air-dried technique, and G bands induced with trypsin (*4*). After treatment with trypsin a few slides were stained with Giemsa to ensure that G band induction was properly done. The various histone fractions (Sigma) and cytochrome c (Sigma) were dissolved in 5 m*M* $MgCl_2$ and 50 m*M* tris-HCl, *p*H 7.5, at a concentration of 0.1 or 1 mg/ml. Calf thymus DNA, either native or heat denatured, was dissolved in the above buffer at a concentration of 1 mg/ml. Half of a trypsin G banded slide was treated with the solution containing one of the above proteins or DNA, while the other half was treated with only the buffer. The slides were incubated at room temperature for either 5 or 20 minutes, and treated by one of the following methods prior to staining with Giemsa: (i) rinsed, (ii) trypsinized, or (iii) fixed in methanol and acetic acid (3 : 1) or 0.2*N* HCl for 30 minutes.

The responses of all chromosomes in each experiment were the same, but for the sake of simplicity, we chose to use only the Chinese hamster chromosome 2 to illustrate the staining behavior. In all slides, control sections showed typical G banding (Fig. 1A). When the trypsin-treated section was incubated with the lysine-rich histone fraction, f1, at a concentration of 0.1 mg/ml, G bands were preserved when the preparation was stained with Giemsa (Fig. 1B). However, when similar slides were treated with f1 at 1 mg/ml, not only the G bands disappeared, but the chromosomes did not take up stain at all, giving a ghost chromosome appearance (Fig. 1C). The slightly lysine-rich fraction, f2a, showed similar behavior, that is, G bands were not blocked at a concentration of 0.1 mg/ml (Fig. 1D), but were completely obliterated at 1 mg/ml (Fig. 1E). Unlike f1, the chromosomes incubated with f2a did not give a ghostlike appearance although they were not intensively stained. No demonstrable reaction was noticed when the slightly lysine-rich fraction, f2b, and the arginine-rich fraction, f3, were used for incubation at either of the concentrations and durations used in our experiments (Fig. 1, F and G, respectively). As controls we used the basic protein cytochrome c (Fig. 1H) and the neutral protein egg albumin (not shown). Neither showed any effect on the appearance of G bands. Denatured and native DNA were also ineffective in blocking the G banding.

Our data suggested that the f1 and f2a histone fractions may be involved in the production of G banding of the chromosomes, but each appeared to have a different mode of operation. The f1 histone completely blocks the staining of the chromosomes, whereas f2a does not. In another set of experiments, we used air-dried slides without first subjecting them to trypsin treatment, and treated them with either f1 or f2a, and then stained with Giemsa. The f1 histone here inhibited Giemsa staining

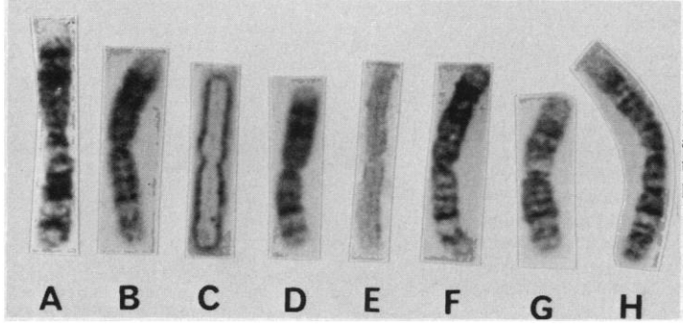

Fig. 1. G banding pattern of chromosome 2 of Chinese hamster fibroblast after treatment with trypsin followed by the protein at the noted concentrations for 5 minutes and finally stained with Giemsa. (A) Control (no protein); (B) f1, 0.1 mg/ml; (C) f1, 1 mg/ml, (D) f2a, 0.1 mg/ml; (E) f2a, 1 mg/ml; (F) f2b, 1 mg/ml; (G) f3, 1 mg/ml; (H) cytochrome c, 1 mg/ml.