

SHORT COMMUNICATION

Seasonal changes in the spatial distribution of phytoplankton in small, temperate-zone lakes

James E. Cloern, Andrea E. Alpine, Brian E. Cole and Terry Heller

US Geological Survey MS496, 345 Middlefield Rd, Menlo Park, CA 94025, USA

Abstract. Seasonal sampling across two small lakes shows that phytoplankton patchiness is greatly enhanced during winter ice-cover relative to the open-water seasons of exposure to wind stress and rapid turbulent mixing.

A fundamental property of plankton populations is their spatial heterogeneity or patchiness. Phytoplankton patchiness can result from spatial variations of biological processes such as growth, grazing, regulated buoyancy and vertical migration (e.g. Reynolds, 1984; Mackas *et al.*, 1985) or from advective transports (George and Edwards, 1976), and it is disrupted by turbulent mixing. These processes are dynamic, so we expect temporal variability of phytoplankton patchiness to accompany fluctuations in physical and biological processes across a spectrum of time scales. For example, fluctuations in the wind stress across small lakes can produce measurable change in the spatial distribution of phytoplankton, at time scales of: hours, associated with the passage of cold fronts (Stauffer, 1982); days, from the cumulative effects of antecedent wind stress over periods of 1–10 days (Small, 1963); and weeks, associated with events of enhanced vertical mixing from weather systems, which have 10–20 days periodicity (Trimbee and Harris, 1983). These observations demonstrate a dynamic coupling between the input of turbulent kinetic energy from wind and the pattern of phytoplankton spatial distribution, operating at time scales of weeks or less. Can this generality be extended to longer time scales? For example, if phytoplankton spatial patterns are responsive to hourly–daily fluctuations in wind stress, then we might expect very large changes in the distribution of phytoplankton when temperate lakes freeze over and become isolated, for months, from the input of wind energy.

To test this hypothesis we mapped phytoplankton biomass (as chlorophyll *a* concentration) seasonally within two small lakes situated in the glacial terrain of northern Minnesota, USA (47°N, 95°W): Williams Lake (surface area 0.4 km²) and Shingobee Lake (surface area 0.7 km²). We measured variability among surface samples collected at 15 or 19 sites distributed across each lake (see Figure 2). Identical sampling was done during: (i) the spring period of incipient thermal stratification (April 1989); (ii) the summer period of maximum thermal stratification (August 1989); (iii) the autumn isothermal period following the breakdown of thermal stratification (October 1989); and (iv) the winter period of ice cover (February 1990). Hence this study was designed to characterize

changing patterns of phytoplankton distribution at the spatial scale of ≈ 200 m and the time scale of months.

Water samples were collected at 0.5 m depth with a Niskin bottle, and aliquots were analyzed for chlorophyll a concentration and particulate carbon (PC). Horizontal sampling was completed within an hour, except during winter when ice augering slowed the sampling to ~ 2 h. One liter aliquots from each sample were collected onto 47 mm A/E glass fiber filters. These were ground and extracted with 90% acetone for spectrophotometric determination of chlorophyll a (Lorenzen, 1967). Smaller aliquots (50–100 ml) were collected onto precombusted 13 mm GF A/E filters, and these were used for determining PC concentration with a Perkin Elmer 240 B Elemental Analyzer. At selected sites, aliquots were preserved in Lugol's fixative and later examined microscopically to determine phytoplankton composition and biomass as biovolume. At the deepest (10 m) site in each lake we also measured vertical variation in chlorophyll a concentration at 1 m depth intervals. On the days before and after the chlorophyll mapping, we measured phytoplankton primary productivity with ^{14}C uptake, using 24 h in situ incubations at eight depths in the euphotic zone (all methods are identical to those described in detail by Cloern *et al.*, 1983). Wind speed and direction were measured hourly from 2 m above the center of each lake (T.C. Winter, unpublished data), and temperature profiles were obtained with thermistors as part of this seasonal study and monthly or semi-monthly by J.W. LaBaugh (unpublished data).

Although the physical structure of Williams Lake changed substantially during the open-water seasons (see temperature distributions, Figure 1), phytoplankton biomass was nearly uniformly distributed across the lake during the spring, summer and autumn sampling periods (Figure 2). On each occasion the range of near-surface chlorophyll a concentrations was less than the mean concentration, indicating a small degree of horizontal patchiness or aggregation (mean daily wind speeds at the times of open-water sampling ranged from 2 to 5 m s $^{-1}$; Figure 1). Vertical gradients of chlorophyll a were small above the thermocline, and we presume that the horizontal samples were representative of local chlorophyll a concentrations within the epilimnion. After more than 2 months of ice cover and isolation from wind stress, the pattern of phytoplankton distribution changed dramatically in Williams Lake (Figure 2, winter). The winter sampling showed a pronounced under-ice horizontal variability manifested (apparently) as one localized patch of high biomass (>30 mg m $^{-3}$ chlorophyll a); location of this patch was not associated with local variations in ice thickness (mean 60 cm) or depth of snow cover (mean 15 cm). Parallel seasonal changes occurred in Shingobee Lake (Figure 2), with a localized patch of high biomass observed under ice, and more uniform distributions during the seasonal periods of exposure to wind stress (note, however, the spatial pattern in spring, which may indicate relict winter patchiness; this lake was sampled only 3 days after ice breakup). The winter patches were composed of different phytoplankton communities in each lake. In Williams Lake, the under-ice population was dominated by an assemblage of flagellates including cryptophytes, chlorophytes and the euglenophyte *Trachelomonas hispida* (Table I).

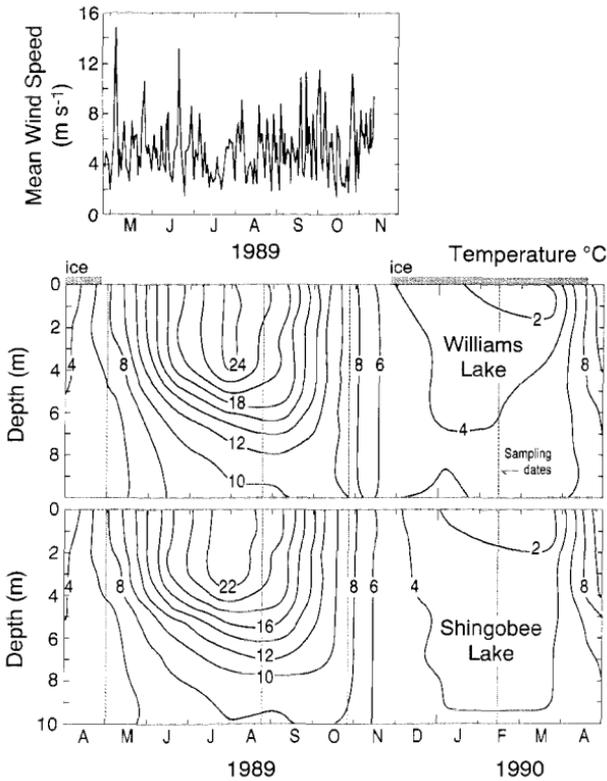


Fig. 1. Vertical contour plots showing seasonal changes in the temperature distribution at the deepest location of Williams and Shingobee Lakes. Upper panel shows mean daily wind speed, measured from 2 m above Williams Lake during the open-water seasons.

However, in Shingobee Lake the winter bloom was composed primarily of the cyanophyte *Oscillatoria amoena*.

Mean phytoplankton biomass varied seasonally by a factor of 6 in Williams Lake and a factor of 2 in Shingobee Lake, but a simple measure of spatial heterogeneity, the ratio of sample variance (V) to mean (m) varied by more than two orders of magnitude (Table 1). David and Moore (referenced in Pielou, 1969) proposed a quantitative measure of patchiness, their 'index of clumping' $I = (V/m - 1)$, which can be used to compare the degree of aggregation, or patchiness, among separate populations. Using their criteria, we conclude that the degree of phytoplankton patchiness during winter, under ice cover, was significantly different from the degree of patchiness observed during the open-water seasons for both lakes (Table I). Although our measurements represent coarse-resolution (in time and space) sampling, they are consistent with the hypothesis that spatial pattern, just like biomass and community composition (Table I), can be a seasonally dynamic property of phytoplankton populations.

Seasonal changes in the vertical distribution of phytoplankton are well-documented for temperate lakes (e.g. Reynolds, 1984; Harris, 1986), but

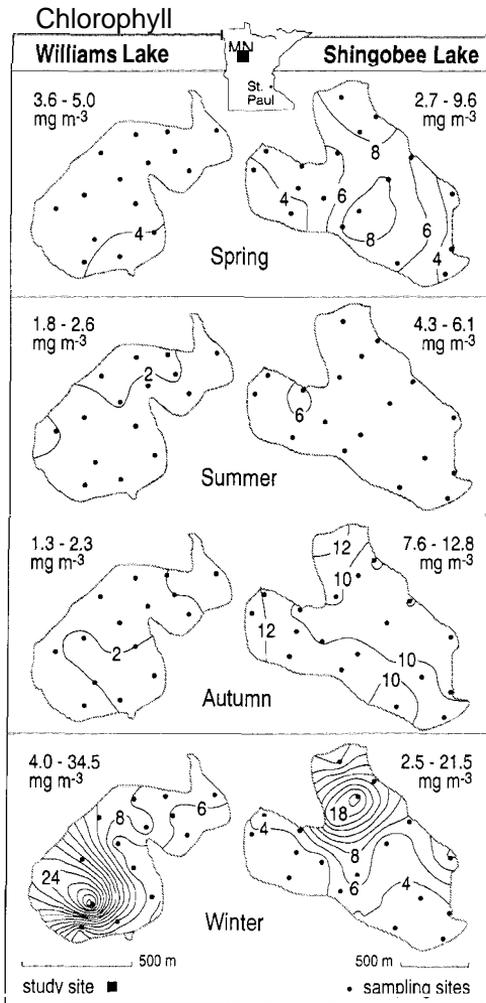


Fig. 2. Horizontal contour plots showing near-surface chlorophyll a distribution across Williams and Shingobee Lakes. Points show sampling locations; contour interval is every 2 mg m⁻³ chlorophyll a. The range of chlorophyll a measurements is also given for each seasonal sampling.

corresponding changes in horizontal patchiness are not. The seasonal changes in horizontal distribution observed in Williams and Shingobee Lakes are, however, consistent with the simplest theories of patchiness. The 'KISS' model (from pioneering papers of Kierstead and Slobodkin, 1953, and Skellam, 1951) describes the horizontal distribution of phytoplankton biomass as a function of exponential growth (at rate μ) and turbulent diffusion parameterized as an eddy diffusivity D :

$$\partial B / \partial t = \mu B + D[\partial^2 B / \partial x^2] \tag{1}$$

Table 1. Seasonal measures of phytoplankton distribution across Williams and Shingobee Lakes

Sampling period	m	V/m	I	Dominant taxa
Williams Lake ($n = 15$ sites)				
Spring Apr. 30, 1989	4.4	0.04	-0.96	<i>Chlorella ellipsoidea</i> <i>Cryptomonas marsonii</i> <i>Rhodomonas minuta</i>
Summer Aug. 22, 1989	2.2	0.04	-0.96	<i>Aphanothece</i> sp. <i>Anabaena</i> spp. <i>Aphanocapsa elachista</i>
Autumn Oct. 18, 1989	1.9	0.06	0.94	<i>Cryptomonas marsonii</i> <i>Cryptomonas rostratiformis</i>
Winter Feb. 14, 1990	11.1	8.5	+7.5*	<i>Cryptomonas marsonii</i> <i>Cyclotella comta</i> <i>Trachelomonas hispida</i>
Shingobee Lake ($n = 19$ sites)				
Spring May 1, 1989	5.9	0.93	-0.07	<i>Rhodomonas minuta</i> <i>Cryptomonas marsonii</i> <i>Fragilaria crotonensis</i>
Summer Aug. 23, 1989	5.4	0.05	0.95	<i>Chryso-sphaerella longispina</i> <i>Anabaena fusca</i>
Autumn Oct. 20, 1989	10.3	0.21	-0.79	<i>Oscillatoria arnoena</i> <i>Cryptomonas ovata</i> <i>Aphanizomenon flos-aquae</i>
Winter Feb. 14, 1990	6.9	5.2	+4.2*	<i>Oscillatoria arnoena</i>

*Significantly different ($P < 0.05$) from the other three seasons, using criteria described in Pielou (1969, p. 92).

m is mean chlorophyll a concentration (mg m^{-3}); V is sample variance; I is David and Moore's index of clumping ($V/m - 1$).

where x is length along the spatial domain. With appropriate boundary conditions, the solution to equation (1) yields a length scale (Okubo, 1984):

$$L_c = 4.81[D/\mu]^{1/2} \quad (2)$$

where L_c defines the critical diameter of a circular patch. For given values of μ and D , patches $< L_c$ cannot be maintained because biomass diffuses away faster than it is produced within the patch.

From our measures of phytoplankton primary productivity, we can estimate seasonal changes in μ in Williams and Shingobee Lakes. From mixing studies in other temperate-zone lakes we can estimate the magnitude of the horizontal eddy diffusivity D , and then calculate critical patch sizes for the seasonal extremes in horizontal mixing rates. The population growth rate μ was calculated as primary productivity in the euphotic zone ($\text{mg C m}^{-2} \text{ day}^{-1}$), normalized by phytoplankton biomass (as mg C m^{-2}). Biomass was estimated as the depth-integrated chlorophyll a concentration multiplied times the phytoplankton C:Chl a ratio in the epilimnion, where the C:Chl a ratio was taken as the slope of the linear regression of PC against chlorophyll a . The annual mean C:Chl a ratio was $51 \text{ mg C mg}^{-1} \text{ Chl } a$ for Williams Lake and 47 for Shingobee Lake. Calculated growth rates ranged from 0.13 to 0.25 day^{-1} during the open-

Table II. Seasonal changes in the estimated phytoplankton population growth rate μ , horizontal eddy diffusivity D , and the corresponding critical patch length L_c (equation 2). The open-water seasons include the range of μ from replicate productivity measurements in each lake during April, August and October 1989

	μ (day ⁻¹)	D (m ² day ⁻¹)	L_c (m)
Williams Lake			
Open-water seasons	0.13–0.25	4.8×10^4	2100–2900
Winter ice-cover	0.04	4.1	50
Shingobee Lake			
Open-water seasons	0.14–0.24	6.8×10^4	2600–3400
Winter ice-cover	0.01	4.1	100

water seasons, and from 0.01 to 0.04 day⁻¹ in winter (Table II). For the open-water seasons of exposure to wind stress, the horizontal eddy diffusivity was estimated from the empirical equation of Boyce (1974), which reflects the scale dependence of turbulent diffusion:

$$D \text{ (cm}^2 \text{ s}^{-1}\text{)} = 1.36 \times 10^{-3} L^{1.36} \quad (3)$$

where L is a mixing length scale (here, L was taken as the mean diameter of 7.2×10^4 cm for Williams Lake and 9.4×10^4 cm for Shingobee Lake). For the winter condition of zero wind stress, we used the value $D = 0.47 \text{ cm}^2 \text{ s}^{-1}$ ($= 4.1 \text{ m}^2 \text{ day}^{-1}$), derived from tracer experiments conducted under ice cover in another small temperate-zone lake (Colman and Armstrong, 1983).

Although the biological potential for horizontal patchiness is greatest during the open-water seasons (large μ), this potential is not realized because turbulent diffusion occurs faster than population growth. Estimated critical patch sizes during the open-water seasons are on the order of 2000–3000 m (Table II), longer than the greatest dimension of these lakes. Hence when the lakes are exposed to wind stress, turbulent diffusion prevents algal patchiness; the KISS model is therefore consistent with the horizontal uniformity observed during the open-water seasons. However, when the lakes are isolated from the input of wind energy and the eddy diffusivity is greatly reduced, the critical patch length L_c becomes much smaller (≤ 100 m, Table II). Even though population growth rates are slow in winter, the time scale of population growth under ice ($1/\mu = 25\text{--}100$ days) is fast relative to that for horizontal diffusion ($L^2/D > 10^5$ days), so small patches can be maintained under ice cover. The calculated values of L_c are of comparable magnitude to the patch diameters observed in winter (Figure 2).

Although the KISS model is a useful conceptual framework for interpreting seasonal changes in plankton spatial distributions, it is an oversimplification that leaves several questions unresolved. First, the KISS model provides no insight into the mechanisms of phytoplankton bloom or patch formation under ice as observed in these two lakes. We speculate that horizontal patchiness under ice may result from the mechanical retention of plankton by thermally driven

circulation of cells (e.g. Welch and Bergmann, 1985). However, advective transport is not included in the KISS model as used here, and we have no direct evidence of such winter circulations in Williams or Shingobee Lakes. Second, we note that extreme horizontal patchiness has been observed in small lakes even during periods of exposure to wind stress, but only under (transitory?) conditions of stable advective flow patterns generated by light winds ($<3 \text{ m s}^{-1}$) when buoyant algal accumulate downwind (e.g. George and Edwards, 1976). This advective patchiness, resulting from horizontal transport and vertical gradients of phytoplankton biomass, also cannot be described with the simple KISS model (Reynolds, 1984). Finally, the analysis here of a bulk measure of phytoplankton biomass (chlorophyll *a* concentration) does not address the differential spatial patterns that exist among individual species (Trimbee and Harris, 1983). However, the observations presented here do demonstrate that the seasonal isolation of temperate lakes from the input of wind energy by ice cover can produce a physical environment that promotes spatial heterogeneity of plankton, and they provide an example of how scales of biological variability can be related to scales of physical variability (Denman and Powell, 1984).

As a final practical comment, the under-ice phytoplankton patchiness observed here implies that other reactive constituents, such as dissolved gases, nutrients or zooplankton, might also exhibit a high degree of spatial variability during winter. Hence sampling regimes for characterizing the plankton community or biogeochemistry of temperate lakes should be designed with a consideration of this potential for seasonal changes in horizontal variability. This is especially relevant for those high latitude lakes where most of the annual phytoplankton production occurs during the period of ice cover (e.g. Welch *et al.*, 1989).

Acknowledgements

We thank Sally Wienke for chlorophyll and PC analyses, and Richard Dufford for phytoplankton enumerations and identifications presented here. We also thank Steve Monismith, Tom Powell, Jim Kuwabara and Jim LaBaugh for their thoughtful reviews of this paper. Tom Winter kindly provided wind data and Jim LaBaugh kindly provided lake temperature data used here.

References

- Boyce, F.M. (1973) Some aspects of Great Lakes physics of importance to biological and chemical processes. *J. Fish. Res. Bd Can.*, **31**, 689–730.
- Cloern, J.E., Cole, B.E. and Oremland, R.S. (1983) Autotrophic processes in meromictic Big Soda Lake, Nevada. *Limnol. Oceanogr.*, **28**, 1049–1061.
- Colman, J.A. and Armstrong, D.E. (1983) Horizontal diffusivity in a small, ice-covered lake. *Limnol. Oceanogr.*, **28**, 1020–1026.
- Denman, K.L. and Powell, T.M. (1984) Effects of physical processes on planktonic ecosystems in the coastal ocean. *Oceanogr. Mar. Biol. Ann. Rev.*, **22**, 125–168.
- George, D.G. and Edwards, R.W. (1976) The effect of wind on the distribution of chlorophyll *a* and crustacean plankton in a shallow eutrophic reservoir. *J. Appl. Ecol.*, **13**, 667–690.
- Harris, G.P. (1986) *Phytoplankton Ecology: Structure, Function and Fluctuation*. Chapman and Hall, London, 384 pp.

- Kierstead, H. and Slobodkin, L.B. (1953) The size of water masses containing plankton bloom. *J. Mar. Res.*, **12**, 141–147.
- Lorenzen, C.J. (1967) Determination of chlorophyll and pheopigments: spectrophotometric equations. *Limnol. Oceanogr.*, **12**, 343–346.
- Mackas, D.L., Denman, K.L. and Abbott, M.R. (1985) Plankton patchiness: biology in the physical vernacular. *Bull. Mar. Sci.*, **37**, 652–674.
- Okubo, A. (1984) Critical patch size for plankton and patchiness. In Levin, S.A. and Hallam, T.G. (eds), *Mathematical Ecology*. Springer-Verlag, Berlin. pp. 456–477.
- Pielou, E.C. (1969) *An Introduction to Mathematical Ecology*. Wiley-Interscience, New York, 286 pp.
- Reynolds, C.S. (1984) *The Ecology of Freshwater Phytoplankton*. Cambridge University Press, Cambridge, 384 pp.
- Skellam, J.G. (1951) Random dispersal in theoretical populations. *Biometrika*, **38**, 196–218.
- Small, L.F. (1963) Effect of wind on the distribution of chlorophyll *a* in Clear Lake, Iowa. *Limnol. Oceanogr.*, **8**, 426–433.
- Stauffer, R.E. (1982) Wind stress effects on chlorophyll distribution in stratified eutrophic lakes. *Limnol. Oceanogr.*, **27**, 66–74.
- Trimbee, A.M. and Harris, G.P. (1983) Use of time-series analysis to demonstrate advection rates of different variables in a small lake. *J. Plankton Res.*, **5**, 819–833.
- Welch, H.E. and Bergmann, M.A. (1985) Water circulation in small arctic lakes in winter. *Can. J. Fish. Aquat. Sci.*, **42**, 506–520.
- Welch, H.E., Legault, J.A. and Kling, H.J. (1989) Phytoplankton, nutrients, and primary production in fertilized and natural lakes at Saqvaqjuac, N.W.T. *Can. J. Fish. Aquat. Sci.*, **46**, 90–107.

Received on September 30, 1991; accepted on January 17, 1992