Abstracta Botanica 17(1-2): 251-260, 1993

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A localized bloom of *Dinobryon sociale* in Lake Balaton: Some implications for the perception of patchiness and the maintenance of species richness

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Keywords: Chrysophyte bloom, Horizontal water currents, Patch generation and dissipation, Spatial pathciness, Species richness.

Abstract: In this paper, we describe an unusual vernal bloom of *Dinobryon sociale* EHRENB. (Chrysophyta, Chrysomonadales) in the plankton of Lake Balaton, Hungary, in 1993. The event was aberrant for two reasons, both of which would have appealed to the scientific curiosity of our late colleague, Pál Juhász-Nagy: one is that the alga seems ecologically unsuited to the environmental characteristics of Balaton and, indeed, has been recorded hitherto only sporadically. The second is that the 1993 bloom had a very localized origin - a near shore area subject to dredging operations - and the rapid growth of the inoculum did much to perpetuate a strongly patchy distribution with respect to the dispersion of the species in the whole eastern lake area. The observations are relevant to the perception and evaluation of patchy distributions and to the importance of measuring them at the appropriate spatial and temporal scales. They also raise once again important conceptual questions about the maintenance of species richness, diversity and rarity.

Introduction

> *"Scaling problems almost everywhere"*
> P. Juhász-Nagy

In this paper, we describe an unusual vernal bloom of *Dinobryon sociale* EHRENB. (Chrysophyta, Chrysomonadales) in the plankton of Lake Balaton, Hungary, in 1993. The event was aberrant for two reasons, both of which would have appealed to the scientific curiosity of our late colleague, Pál Juhász-Nagy: one is that the alga seems ecologically unsuited to the environmental characteristics of Balaton and, indeed, has been recorded hitherto only sporadically. The second is that the 1993 bloom had a very localized origin - a near shore area subject to dredging operations - and the rapid growth of the inoculum did much to perpetuate a strongly patchy distribution with respect to the dispersion of the species in the whole eastern lake area. The observations are relevant to the perception and evaluation of patchy distributions and to the importance of measuring them at the appropriate spatial and temporal scales. They also raise once again important conceptual questions about the maintenance of species richness, diversity and rarity. As these are all topics which have engaged the attention of Pál Juhász-Nagy (1992, 1993), we are pleased to dedicate this contribution to his memorial volume.

Lake Balaton and its phytoplankton

Balaton (47° 3' 50" - 46° 42' 6"N, 17° 14' 58" - 18° 10' 28"E) is the largest shallow lake in central

Europe. The lake has a surface area of 593 km^2, is 77.9 km long, 9 km wide on average, and has a mean depth of 3.14 m (maximum 11 m); its surface has an altitude of 104.5 m.a.s.l. The theoretical retention time of the lake is between 3 and 8 years. The lake water has a high alkalinity and is well buffered against pH fluctuation. It was originally mesotrophic but underwent rapid enrichment during the 1970s.

Regular weekly sampling for phytoplankton has been maintained since 1989 at an open-water station in front of the Balaton Limnological Institute (Fig. 1). Its seasonal abundance is characterized by two peaks (Figs 2- 3). The first develops in spring and it is normally dominated by diatoms, especially *Cyclotella radiosa* HÅKANSSON, formerly referred to *Cyclotella comta* (EHR.) KÜTZ., and *Synedra acus* KÜTZ. The spring bloom peaks at a fresh mass of around 5 mg l^{-1}. The second maximum, usually in September or October, comprises several 'regular' species of blue-green algae: *Lyngbya limnetica* LEMM., *Aphanizomenon flos-aquae* (L.) RALFS, *A issatschenkoi* (USAK.) PROSCH.-LAVR., *Anabaena aphanizomenoides* FORTI, *Cylindrospermopsis raciborskii* WOLOSZ., *Planktothrix agardhii* (GOMONT) ANAGN. & KOMÁREK. The peak populations, dominated by *Cylindrospermopsis raciborskii* have exceeded 40 mg l^{-1} on occasions.

Besides these 'key' species, others have been noted to have occurred either regularly in small numbers or occasionally in an abundance but, hitherto, the Chrysophytes have been poorly represented in Balaton (Padisák 1992). The observation is consistent with the general understanding of their ecology and the environmental characteristics of Balaton. Certainly, the more conspicious genera

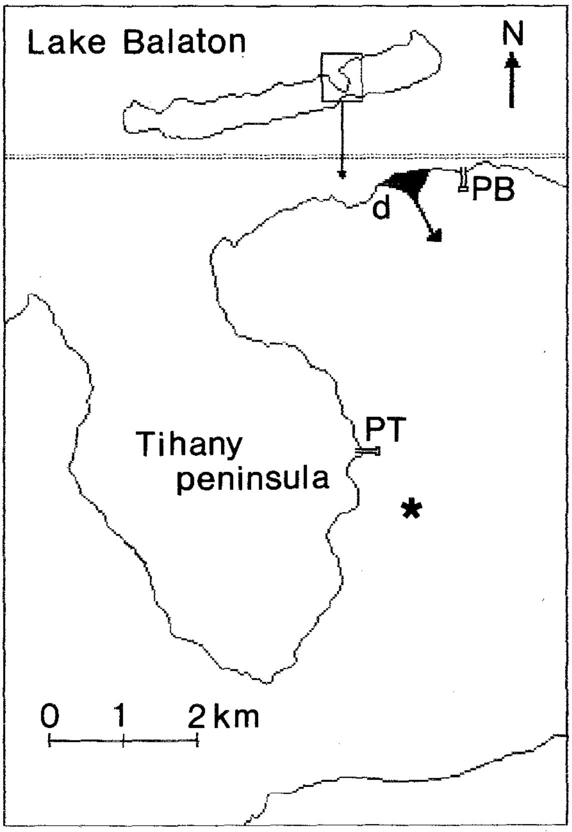

Figure 1. Lake Balaton and the Tihany peninsula. PB: Port of Balatonfüred; PT: port of Tihany; black spot with an arrow: the place of soft mud removal and the direction of pumping into the open water; sampling station for weekly sampling is indicated with an asterisk

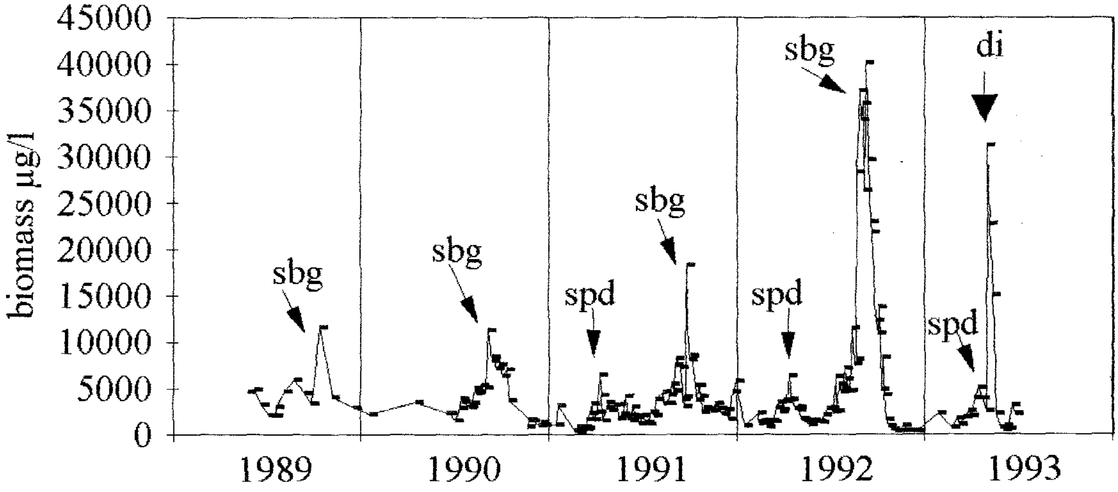

Figure 2. Quantitative changes of phytoplankton biomass in Lake Balaton at Tihany in 1989-1993. Abbreviations - sbg: summer blue-green bloom; spd: spring diatom bloom; di: *Dinobryon* bloom.

of chrysomonads occur widely in smaller European oligotrophic lakes, usually having low alkalinity, and a neutral or slightly acidic pH (Reynolds 1988; Sandgren 1988) where they are relatively most abundant following the decline of the spring diatom phase (Dokulil & Skolaut 1991). A long standing belief that chryso-phytes were obligately confined to waters of low phosphorous content (e.g., Rodhe 1948) has been disproved experimentally (Lehman 1976) and, besides, it is confounded by the observed distribution of many of the same species in enriched, sometimes quite alkaline, farm ponds with prevalent organic deposition (Reynolds 1971, Sandgren 1988), where they usually show a marked seasonality of abundance. Selected chrysophytes have been shown to have high affinity for low ambient concentrations of inorganic phosphate and a capacity to absorb organically bound phosphate; they can also obtain nitrogen from both inorganic sources (nitrate, ammonia) and organic (urea, glycine, adenylic acid: Lehman 1976) sources. Their ability to utilize these organic sources and a reported capacity for phagotrophy (Pascher 1943, Bird & Kalff 1986, 1987) suits them to water columns in which the products of organic breakdown including, in rarified open-water habitats, the death and decline of a previous bloom, are available. Moreover, the repeated observation of Reynolds (1986) of chrysophyte sensitivity to upward pH-drift in low-alkalinity waters of the English Lake District has been substantiated by recent research by Saxby (1990 and in preparation): there is a demonstrable inability of *Dinobryon* and *Synura* to function vegetatively without a supply of free carbon dioxide.

It is this last point which makes the mass development of *Dinobryon* in Balaton especially remarkable. The high bicarbonate alkalinity of the lake (3.70 ± 0.73 meq l^{-1}) is such to buffer the ambient pH within the range of 8.6-8.7. There is effectively no reserve of free carbon dioxide maintained at this level.

Features of the *Dinobryon* bloom of 1993

Dinobryon sociale was first recorded in Balaton by Hortobágyi (1942, 1943) and it has been noted frequently in samples since then (Hortobágyi 1951, 1977, Tamás 1959, 1964, 1967, 1969, 1972, 1975, Padisák 1980, Németh & Vörös 1986, Uherkovich & Lantos 1987). It was sporadically recorded each year between 1989 and 1992 (Fig. 4) although a greater absolute biomass (~ 300 μg l^{-1}) was noted in 1990. In most instances, however, the species was found to be "very rare": even in studies where quantitative data are given, *D. sociale* is indicated merely by the entry "present". *D. sociale* is nevertheless, the most common species of *Dinobryon* in the lake; others (*D. sertularia* EHRENB., *D. divergens* IMHOF) occur still more sporadically. It is not the taxonomic uncertainty that has restricted *D. sociale* to its erstwhile rarity status!

The 1993 bloom was closely associated with a coastal dredging operation and the pumping of some 4,000 m^3 of soft mud from a 9,600 m^2 section of near-shore deposits, between the ports of Balatonfüred and Tihany (Fig. 1); on average, the upper 40-cm of sediment would have been

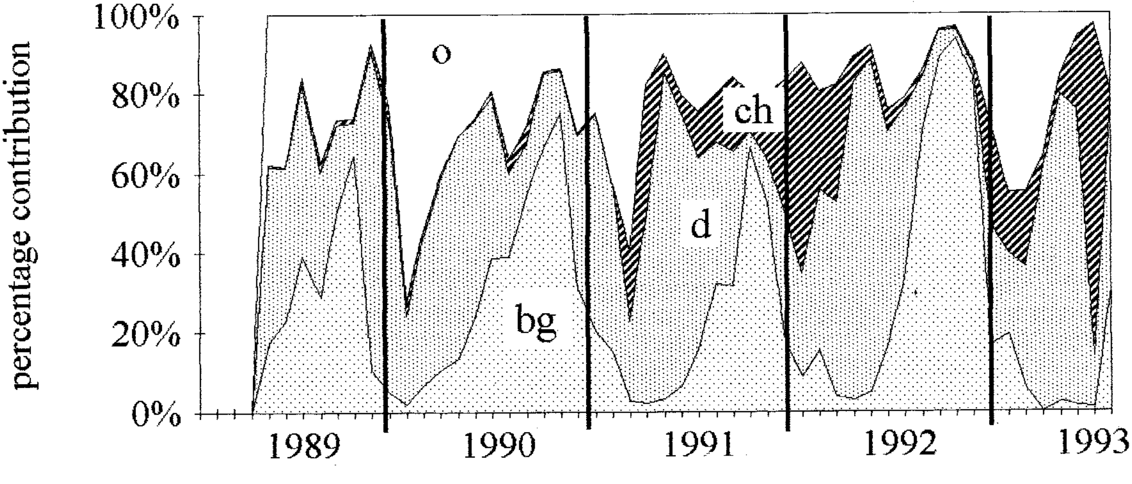

Figure 3. Percentage contribution of different algal groups to total biomass in Lake Balaton at Tihany in 1989-1993. Abbreviations - bg: blue-green algae; d: diatoms; ch: chrysophytes; o: other groups.

removed. The soft-mud suspension was piped some 700 m south east of the dredging area, into the open water of the eastern basin, although the end of the pipe was relocated from time to time supposedly to better disperse the mud. The sediment pumping began on 27 April and was completed by 14 May. The conspicuous mud plume which was created initially followed a visible path close to the eastern shore of the Tihany peninsula, and one of the Institute's regular sampling stations. The unusually large population of *D. sociale* recorded on 2 May (78,500 cells ml^{-1} or 28.2 mg l^{-1}) nominally represented 90 % of the biomass and an eleven-fold increase of *Dinobryon* cell numbers over five days (see Fig 5: specific rate of change: ≥ 0.486, or a net doubling every ≤ 1.4 day).

Further samples were taken at 17 stations on 10 May 1993 to check the growth and dispersion of the *Dinobryon.* All samples were preserved in Lugol's Iodine and counted by inverted microscopy with a precision of $\leq \pm 10$ % (Lund, Kipling & Le Cren 1958). This was quite adequate to establish the significance of the *Dinobryon*-biomass counts noted in Fig. 6a and its markedly non-uniform distribution within the lake. Numbers equivalent to a biomass of 11.4 mg l^{-1} persisted off Tihany and concentrations of 2-3 mg l^{-1} persisted along the north shore of the eastern basin. In open waters, concentrations were 0.3-1 orders of magnitude less while numbers had scarcely ever increased in the western basin. This horizontal distribution calls attention to the role of water currents in dispersing locally developed populations. According to Györke's (1986) detailed investigations, the characteristic subsurface currents are generated during long-lasting episodes of more or less unidirectional wind and persist inertially for some time after the wind action ceases. A predominantly south west wind working down Balaton appears to provide sufficient explanation for the north-eastward forcing of near-surface water (together with the suspended seston) in the eastern basin and a counter-clockwise rotation to the east of the Tihany peninsula and for the eventual dispersal of the mud plume and the *Dinobryon* cells in association therewith.

After its maximum on 2 May, the *D. sociale* population progressively diluted away ("halving time", about 4.3 days) at the Tihany station (Fig. 5) and substantially disappearing elsewhere during the month of May. The production of resting cysts, which precipitate to the bottom mud, was observed to have contributed to the demise of the population. By the beginning of June, only occasional cells and resting cysts survived at any station in the lake.

Any interpretation of these remarkable events needs to account for the sudden recruitment, rapid growth and no less spectacular decline in the *D. sociale* population, bearing in mind the preconceptions about the environmental requirements of the species. Clearly, the initiation of the population was not independent of the sediment pumping. It may well have been the case that the numbers already developed in April represented the periodic ascendancy of *Dinobryon* in the wake of the decline of the spring diatom phase, as familiar in many central European lakes, and near (or anything beyond) the maximal levels the alga achieves in Balaton, wherein the high alkalinity is overriding. On the other hand, the close associa-

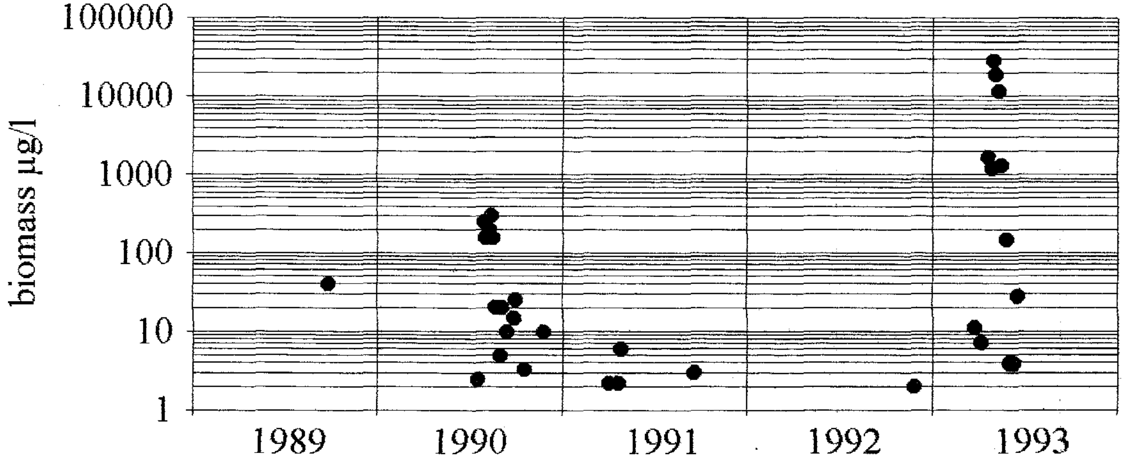

Figure 4. Biomass (log-scale) of *Dinobryon sociale* in Lake Balaton at Tihany in 1989-1993.

tion of explosive increase with the injection into the water of soft sediment was crucial, for several possible and not mutually exclusive reasons.

One is its possible source of *Dinobryon* cysts. Most common planktonic chrysomonads arguably conform to a life-cycle strategy that blends pessimism and opportunism (Sandgren 1988): cysts are not produced exclusively in response to the onset of the legendary adverse conditions but when populations are extant and flourishing. This ensures a reasonably prolific fund of propagules and potential recruits to an extant population when the next opportunity presents itself. Instances of rapid recruitment of excysting chrysophytes on the satisfaction of appropriate growth conditions have been reported occasionally in the literature (Pick, Nalewajko & Lean 1984). Whether this could apply to Balaton would depend upon whether large numbers of cysts were present is the sediments and, if so, over what period of time had they accumulated and remained viable.

Next is that the sediment provided substances or conditions otherwise lacking in the open water to favour *Dinobryon* growth that was otherwise prevented. The organic products which are well represented in the superficial sediments of Balaton (Dobolyi 1980) must be assumed to have been adequate to fulfill the "pond carbon-conditions" referred to above. It is interesting that the initial growth was not only not sustained but was soon reversed, perhaps as a consequence of the rapid dilution of the same factor.

Third, the associated releases of nutrients, especially of soluble phosphorus, could have been critical: the large amounts of iron resident in the sediments and injected into the open water (Fig. 6c) could have had stimulating effect upon *Dinobryon*, in particular (Lehman 1976), although the iron content of Balaton would appear to be sufficient to saturate the growth requirements of most planktonic algae.

Patch generation and dissipation

Whilst the available data do not permit us to resolve the precise causes of a partially measured effect, they do permit us to focus on the perplexing ecological problem of patchiness.

In the case of plankton populations, the issue is complicated by the fact that the suspending medium is fluid and, at first sight, isotropic. Yet here, as on land, the question of uniformity or patchiness reduces to a matter of the spatial and temporal scale at which it is observed (Juhász-Nagy 1992). It is not difficult to accept obvious large differences in the biomass species composition and productivity of the great oceans where gradients in, for instance, temperature, day length and the positions of the landmass distinguish within-latitude circulations and cross-latitude return currents: these have been known for as long as mariners have explored the seas and have only been confirmed by the most modern remote-sensed imagery from satellites. Water depth (especially on the continental shelves), nutrient inputs (from large rivers discharges to the sea) and local

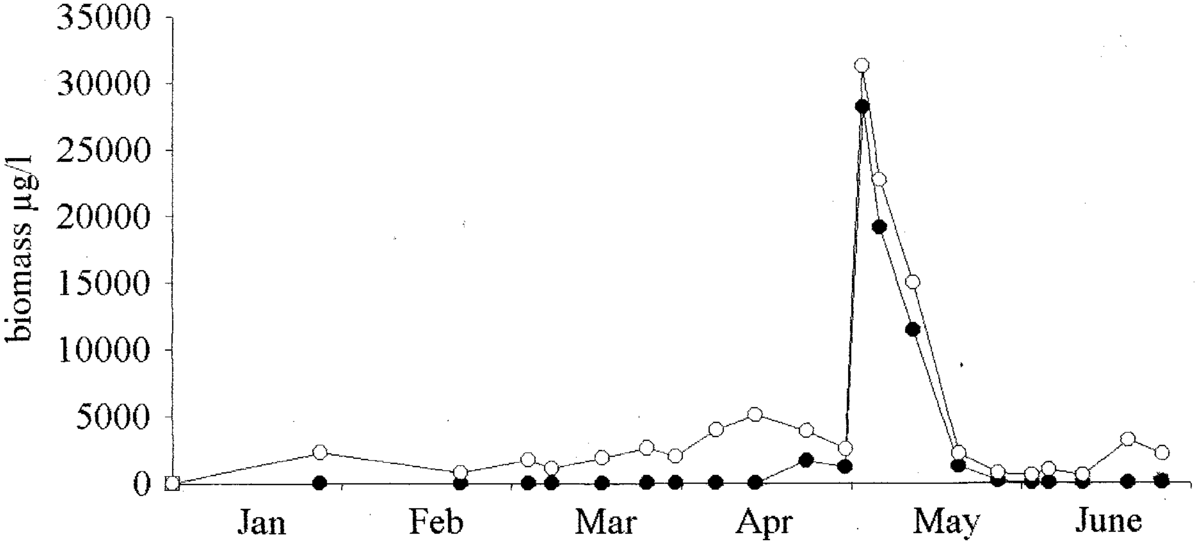

Figure 5. Phytopalnkton biomass (O) and biomass of *Dinobryon sociale* (●) in Lake Balaton at Tihany in January-June, 1993.

boundary mixing (as in fronts) also influence marked localization of plankton abundance at the ocean's edges. Among studies on large freshwater lakes, analogous horizontal segregation of ambient population abundance is less well-known, although those instances demonstrated in lakes Erie (Verduin 1951), Ontario (Munawar & Munawar 1975) and Memphré-magog (Watson & Kalff 1981) are together indicative of comparable processes built on stable gradients of temperature, motion and nutrient concentration.

In smaller lakes, however, the expectations are of uniformity with low coefficients of sample variability (Nasev, Nasev & Guiard 1978; Irish & Clarke 1984) and such significant variations that have been demonstrated are generally assumed to be observable only over short periods and to be contributed by the action of water movements upon the transient behavior of *existing* populations (Small 1963, Sandusky & Horne 1978). This in spite of the fact that the most striking segregations occur in the vertical (stratification), yet depending upon its speed and direction, the effect of wind on weakening vertical stability quickly leads to horizontal patchiness (see especially George & Edwards 1973, George & Heaney 1976, George 1981; the latter includes a revised interpretation of the older observations of Colebrook 1969). A change of wind often induces a new distribution with hours: essentially the *same* material is simply reorganized.

Short-term patchiness is also familiar at the scale of Langmuir rotations: the compacted displacements of a surface drift current and their spiraling returns create a series of upwellings and downwellings, the latter marked by slicks of bubbles (hence their name, 'windrows') and floating particles (e.g., buoyant cyanobacteria) running nearly parallel to the wind, generally at distances of 3-15 m apart. Within the boundaries of the rotations, distributions are recognized to be more nearly uniform - this is the range of the average sampling bottle. Yet if the series is pursued, the scaling reaches the size of the smaller and turbulent eddies (0.5 - 5 mm), with the potential of every viscous patch being briefly different from the next in

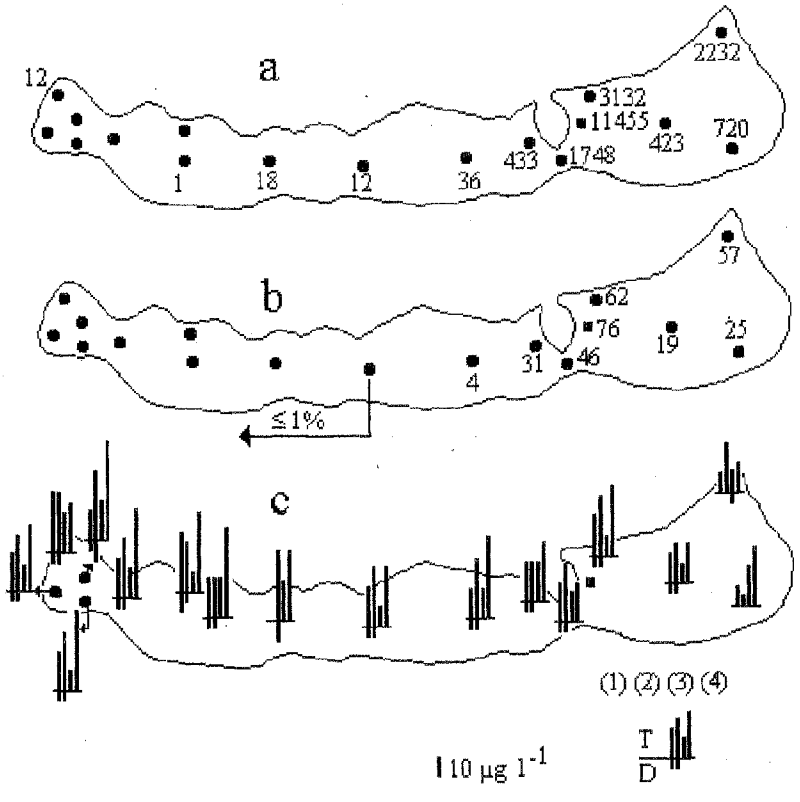

Figure 6a: Horizontal distribution of a: *Dinobryon sociale* (numbers indicate biomasses in $\mu g\ l^{-1}$) on 10 May, 1993; b: contribution of *Dinobryon sociale* to total biomass (numbers are percents) on 10 May, 1993; c: iron concentration on 5 April, 1993 (1), 10 May, 1993 (2), 7 June, 1993 (3) and 7 July, 1993 (4) in Lake Balaton. Abbreviations - T: total iron, D: dissolved iron; bar-length corresponding to an amount of 10 $\mu g\ l^{-1}$ is indicated below the graphs.

the concentration of organisms it bears. Ultimately, at the scale of a few micrometers (the size of the algal cells), patchiness resolves to a presence or absence.

Students of Mandelbrot (1977) will recognize this as a fractal series. At the scale of 1-10 μm, phytoplankton distribution is strongly patchy. In the range of 10 μm - 1 mm, it becomes increasingly random with uniformity at a measurable level of probability. At 1-10 mm, variability in the distribution is subject to organismic swimming speeds and to turbulence, rather than to diffusion: patchiness is very transient in the horizontal plane, any clustering tending to group around the Langmuir scale, but in the vertical, it persists to the temporal scales of growth and cell generation, that is, sufficient to permit the formation of (say) deep-chlorophyll maxima (Reynolds 1992).

The horizontal analogue - a localized patch sustained by the dynamics of cell replication - requires the rate of cell replication to exceed the rate of horizontal dispersive dissipation. Put the other way around, a 'patch' will survive only for so long as its rate of generation exceeds the rate at which is eroded at its edges. Several authors have considered this relationship: the so called 'KISS' MODEL (after Kierstad & Slobodkin 1953 and Skellam 1951) predicts the size of patch that can be maintained against horizontal diffusivity. Its radius (R_c) is given by

$$R_c = 2.4848\ (D/k)$$

where D is the horizontal diffusivity and k the net rate of increase of the population under consideration. When we accord appropriate values to k (initially not less than 0.486 d^{-1}, but falling away to 0.35 d^{-1}: $\leq$ 0.7 doubling per day) and D in respect of wind-driven diffusivities likely to have obtained in Balaton at the time ($\leq 8\ ms^{-1}$: $D \leq 6.4 \times 10^5\ cm^2\ s^{-1}$), a critical patch radius of 22 km is solved; the patch might survive weaker diffusivities (in light winds of 2 m s^{-1}, R_c falls to 1.4 km) but would have to be increasingly large as growth rate slowed down. The point at which dispersion theoretically secured even variability throughout the Eastern Basin would have come when growth rate was about half the maximum.

Considering advective transport of the plume, the model of Joseph & Sendner (1958) gives a more useful measure of the horizontal distance travelled by a dispersing population per division. Again, as a radius,

$$R_c = 3.67\ U_s/k$$

where U_s is the mean advective velocity. For a wind speed of 8 m s^{-1} ($U_s \sim 0.01$ m s^{-1}) R_c solves at $\sim$ 4.5 km; i.e., a patch could not be maintained in a smaller space. At weaker wind speeds, Rc is proportionately smaller, so long as the rate of growth is maintained ($\sim$ 1.1 km when the wind speed is 2 m s^{-1}). but as the growth rate weakens, the theoretical patch soon expands to the size of the entire lake (that is, it ceases to be a distinct patch). As with the KISS calculation, the deductions are not confounded by the observations: the patch, generated at a point source and spreading with recognized horizontal drift currents remained strongly discrete through the 5-10 days that the replication rate was sustained; after which, its identity quickly disappeared.

Rarity and richness: the basis of species diversity

It has been widely recognized that natural lakes can be very rich in phytoplankton species. Many of the species are rather erratic in their appearance and abundance; others are more predictable but still very rare, when compared to the numbers of the few dominant species. Competitive Exclusion Theory (Hardin 1960; Tilman 1982) predicts that only as many species can coexist as there are limiting factors. Hutchinson (1961) termed the apparent contradiction between the number of species and the number of limiting resources the "paradox of plankton". The search for a solution to this apparent paradox has occupied plankton biologists ever since.

Although freshwater biologists associate the problem of species diversity with Hutchinson, it is fair to say that analogous questions have been prevalent among terrestrial ecologists. For instance, Grime (1973) was among the first to recognize that although competition can be a major causal factor in the maintenance of low diversities in herbaceous vegetation, there is nevertheless a low incidence of competitive species in floristically rich habitats. Wilson (1990) considered twelve possible mechanisms to account for species coexistence in New Zealand plant communities: most of these are equilibrium concepts, including niche diversification and stabilizing co-evolution. Non-equilibrium explanations, that are especially relevant for phytoplankton assemblages, assumed that there had not been enough time for competition to completely exclude relevant species before sudden or gradual alterations intervene to arrest or shift back the development of the association of species (Sommer et al. 1993).

The present observations remind us that very few of the species recorded in the plankton of a given lake are ever common: most in fact are quite sporadic in occurrence or are maintained only at background populations. It may be that they represent the 'incompletely excluded' vestiges of some past episode of specific extancy and hence carry forward some community 'memory' of past events (Padisák 1992). However, if we consider that most freshwater plankton species are extremely cosmopolitan, with very little endemism, it is also reasonable to deduce that these distributions attest to high mobility between water bodies. This observation has been recognized often, though never satisfactorily explained: it is clear that whether transported in spray, dust or on or in the bodies of birds and insects, planktonic algae must constantly 'reinfect' water bodies. Just occasionally, they encounter the conditions which favour the establishment of populations.

Whilst the role of resting cysts and propagules is strongly implied in the case of Balaton *Dinobryon* and leans to the 'memory' explanation, it is the temporal heterogeneity of planktonic ecosystem structure which we want to emphasize. While external events continue to intervene at scales between those of generation times and of competitive exclusion, then community structure can be as variable as is the diversity of species to fill it. The complementary deduction is that a rich diversity of species is promoted by a totality of environments which, in the main, are maintained in a condition far short of a competitively excluded steady-state. In lakes, the relevant external events are perceived to be storm and flood events, although they include such natural variability about regular forcing mechanisms as prolonged or unusually stable stratification, drought or chemical enhancement (Reynolds 1993). Vertical discontinuities in deep lakes and horizontal heterogeneity in shallow lakes surrounded by extensive wetlands, through surface-level fluctuations and the extent of macrophyte beds, compound the effects of climate-induced mass transport of water in both types of water body. Thus, spatial patchiness is an integral component of a proper ecological understanding of phytoplankton.

Concluding remarks

The final point we would wish to make is one which has been made previously (Reynolds, Padisák & Sommer 1993). The patterns and processes observable in plankton occur at characteristically small spatial and temporal scales but they remain good models of terrestrial ecosystems. Because such population and community phenomena as dominance, diversity, equitability, vulnerability, exclusion etc. are resolved at the scale of generations and beyond, it follows that their study is greatly facilitated by focusing on the pelagic vegetation, the key units of which have generation times measured in hours to days, rather then terrestrial vegetation, where the corresponding time scales may be tens to hundreds of years. "Scaling problems almost everywhere" (Juhász-Nagy 1992) may yet be turned to advantage of progress in theoretical ecology.

Acknowledgments. The authors thank Dr. Miklós Rajczy for his help in searching for early data on *Dinobryon* in Lake Balaton (on-line data bank Flora et Iconographia Algarum Hungariae; Botanical Department of the Hungarian Natural History Museum). This work was supported by the Hungarian National Science Foundation (OTKA No. 6285).

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