

## Phytoplankton species diversity control through competitive exclusion and physical disturbances

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### *Abstract*

Competitive exclusion theory suggests that phytoplankton species number in an assemblage at equilibrium will be limited to the number of simultaneously limiting resources, generally three or fewer. However, natural phytoplankton assemblages usually exhibit high species diversity, hence the concept of Hutchinson's "paradox of the plankton." Recent works have suggested that this apparent paradox is a result of disturbances intermediate in frequency relative to the time period necessary for species succession to lead to equilibrium conditions (sensu Connell's intermediate disturbance hypothesis [IDH]). Moreover, evidence indicates that disturbances of intermediate intensities are also conducive to maintenance of high species diversity in phytoplankton communities. Using a long-term data record from hypereutrophic subtropical Hartbeespoort Dam (South Africa) that was typically dominated by a single species, but annually subjected to physical disturbance, we demonstrate here that disturbances can indeed enhance phytoplankton species diversity. However, these data fail to support Connell's IDH *per se*, as moderate- and high-intensity disturbances yielded similarly high species diversity. These data also suggest that community resilience (the ability or time to return to predisturbed conditions) is negatively related to disturbance intensity, such that higher intensity disturbances maintained high diversity for longer periods of time relative to lower intensity disturbances.

Competitive exclusion theory (Hardin 1960) suggests that under constant conditions the number of species in a phytoplankton assemblage at equilibrium should be limited to the number of simultaneously limiting resources, generally three or fewer (Sommer et al. 1993). However, natural phytoplankton assemblages are typified by high species richness and diversity (Harris 1986). Hence the "paradox of the plankton" (Hutchinson 1961) has often been used to infer our lack of understanding of factors controlling species diversity in natural phytoplankton assemblages.

Various approaches to solving the apparent paradox recognize that pelagic environments are rarely uniform, especially with regard to resources, and competitive conditions are dynamic such that equilibrium is rarely obtained (Tilman 1982; Sommer 1985; though *see* Peterson 1975). One such approach, pioneered by Reynolds (1988) and recently the subject of an extensive collection of papers (Padisák et al. 1993), has been the adaptation of Connell's (1978) intermediate disturbance hypothesis (IDH). As its name implies, IDH suggests that disturbances of intermediate frequency or intensity can act to maintain high species diversity in communities that would otherwise be dominated by a few su-

perior competitors by allowing early successional "pioneer" species to invade repeatedly.

For phytoplankton assemblages, Reynolds (1988) suggests that high species diversity is maintained by a frequency of disturbance intermediate to the time period necessary for species succession to lead to equilibrium conditions and dominance by a few competitively superior "climactic" species. While attainment of equilibrium conditions by species succession in tropical reefs or forests may take years, decades, or even centuries, species succession in phytoplankton is measured in terms of days to months. Hence, disturbances of ca. 200 h or less in frequency could preserve high species diversity in phytoplankton (Reynolds 1988). Types of disturbances of this nature suggested to enhance species diversity in phytoplankton assemblages include water column mixing due to storms or autumnal cooling and substantial changes in zooplankton grazing pressure (Padisák 1994; Sommer 1995).

Sommer (1993) demonstrated that not only disturbances of intermediate frequency, but of intermediate intensity as well, can maintain high species diversity in phytoplankton assemblages. As a further demonstration of the value of the IDH in phytoplankton ecology, we present here long-term data comparing phytoplankton species responses in nature to two intensities, rather than frequencies, of disturbance. Observed patterns in a 7-yr record of the phytoplankton in a hypereutrophic reservoir give support to the alternating roles of competitive exclusion and physical disturbances in regulating species diversity in phytoplankton assemblages.

### Methods

*Study site and background*—Hartbeespoort Dam, a small (20 ha,  $170 \times 10^6$  m<sup>3</sup>, 34 m maximum depth) subtropical impoundment of the Crocodile River near Johannesburg,

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South Africa, was first described by Hutchinson et al. (1932) as oligotrophic with a phytoplankton assemblage dominated by the dinoflagellate *Peridinium cinctum*. Owing to heavy nutrient loading from sewage and domestic effluents (Scott et al. 1980; Chutter 1989) during the period since Hutchinson's visit, the productivity of Hartbeespoort Dam increased to a level of hypertrophy. By the 1970s the reservoir was characterized by massive water hyacinth (*Eichhornia crassipes*) cover. Following herbicidal eradication of the hyacinth in 1978 (Scott et al. 1979), abundant phytoplankton developed and became dominated by the cyanobacterium *Microcystis aeruginosa* (hereafter *Microcystis*). Since 1979, *Microcystis* has typically dominated the phytoplankton for 6–10 months each year (Scott et al. 1980; Zohary and Robarts 1989, 1990; Zohary et al. 1996). During this extended period of *Microcystis* dominance, ca. 90% of the total algal biomass (as chlorophyll) was contained within the upper 4 m of water such that little light penetrated to depth and few other species proliferated. In autumn and winter, *Microcystis* formed dense surface hyperscums up to 75 cm thick in wind-protected bays, often covering several hectares in surface area (Zohary 1985; Zohary and Breen 1989).

Beginning in 1985, management efforts were made to curtail the extent of hypertrophy and of *Microcystis* blooms in Hartbeespoort Dam and in the Transvaal Highlands in general. A 1 mg L<sup>-1</sup> phosphorus (P) restriction on all domestic and industrial effluents was enacted, resulting in a gradual reduction in P loading to the Hartbeespoort Dam catchment during the late 1980s, with subsequent decreases in P concentrations in the lake. In addition to reduced P loading, refilling of Hartbeespoort Dam in 1987 following 5 yr of drought enhanced the reduction in P concentrations in the lake by ca. 50%, with an increase in water column N:P ratios by nearly fourfold (Chutter 1989; Chutter and Rossouw 1991). A further remedial step taken for Hartbeespoort Dam was the repeated flushing of *Microcystis* hyperscums over the dam wall in 1987 and 1988 (Zohary et al. 1996).

*Phytoplankton analysis*—Phytoplankton species composition and abundances, together with zooplankton and a range of physical and chemical parameters, were determined weekly or biweekly during 1982–1988 in Hartbeespoort Dam. Details of the full monitoring program, methods employed, and data obtained can be found elsewhere (NIWR 1984; Chutter 1989; Zohary et al. 1996). Details regarding phytoplankton monitoring and analyses have been reported by Zohary et al. (1996), but are briefly summarized here.

Water samples were collected at weekly (May 1982–December 1986) or biweekly (January 1987–December 1988) intervals between 0900 and 1100 h in the lake's main basin using a 6-liter vanDorn sampler from 0, 0.5, 1, 2, 3, 4, 5, 6, and 8 m. A depth-integrated sample was created using equal volume aliquots of each discrete-depth sample. A portion of the integrated sample was immediately fixed with Lugol's iodine for cell enumeration; the rest was kept fresh for species identification and measurement of cell linear dimensions the following day.

Phytoplankton cell numbers were enumerated with an inverted microscope at ×500 magnification after sedimenting (for 24 h) a 1–10-ml subsample of the preserved sample, or

a known dilution thereof, in glass sedimentation chambers (Lund et al. 1958). *Microcystis* was counted using separate subsamples that had been subjected to agitation in an Ultra-Turrax blender (10–30 s at 20,000 rpm) prior to sedimentation (Zohary and Pais-Madeira 1987).

Initially (May 1982–October 1983), counting precision ranged between 10 and 20% for dominant taxa. Five fields of vision and a total of at least 400 cells per sample were counted (Lund et al. 1958). From November 1983 onward, the counting method was modified according to Lewis (1978) in order to increase the precision for estimating numbers and biomass of less common taxa. One hundred cells of each species or 100 fields of vision, whichever came first, were counted. Cell volumes were calculated from linear dimensions of cells in fresh samples using geometric equivalents. At least 20 individuals of each species were measured in each sample. The median cell volume for each species was used for conversion of cell numbers to volumes (Rott 1981). Wet weight biomass was then calculated assuming a specific density of 1 g cm<sup>-3</sup>.

Changes in phytoplankton dynamics were also examined using Shannon's diversity index, H', calculated from the biomass data as

$$H' = - \sum_{i=1}^s p_i \cdot \log_2 p_i \quad (1)$$

where  $p_i$  is the relative biomass of species and  $i$  and  $s$  are the number of species (Sommer 1993). Data prior to January 1984 were excluded from calculations of H'.

## Results

*Competitive exclusion versus intermediate disturbance*—During 1982–1988, 73 species were identified in the phytoplankton assemblage of Hartbeespoort Dam. Only 20 species were seasonally abundant, and the number of coexisting species was generally low ( $N_{\text{mean}} = 17$ ) (Zohary et al. 1996). Total phytoplankton biomass was generally high, reaching as much as 160 g (WW) m<sup>-3</sup> (excluding hyperscums) (Fig. 1). Strong horizontal patchiness in the *Microcystis* distribution created large apparent temporal variability in estimated standing stock generally unrelated to growth and mortality (Zohary and Robarts 1989). Until mid-1987, cyanobacteria, primarily *Microcystis*, were dominant for 6–10 months each year. The seasonal pattern of *Microcystis* domination varied from year to year. Generally, the population increased rapidly in late spring and early summer (October–December), reaching a peak in biomass in summer (January–March). This large standing biomass was maintained throughout autumn and most of winter, although there was little net growth during winter (Zohary and Robarts 1990). During periods of *Microcystis* domination, other species rarely proliferated, exceptions being the cyanobacterium *Pseudoanabaena*, which grew in association with the *Microcystis* colonies, and a few diatoms and cryptophytes (Zohary et al. 1996). Grazing by zooplankton, dominated by small-bodied cladocerans (*Ceriodaphnia* sp.), was characteristically low during the *Microcystis* season (Jarvis 1986; Jarvis et al. 1988).

In late winter and early spring (August–September) each

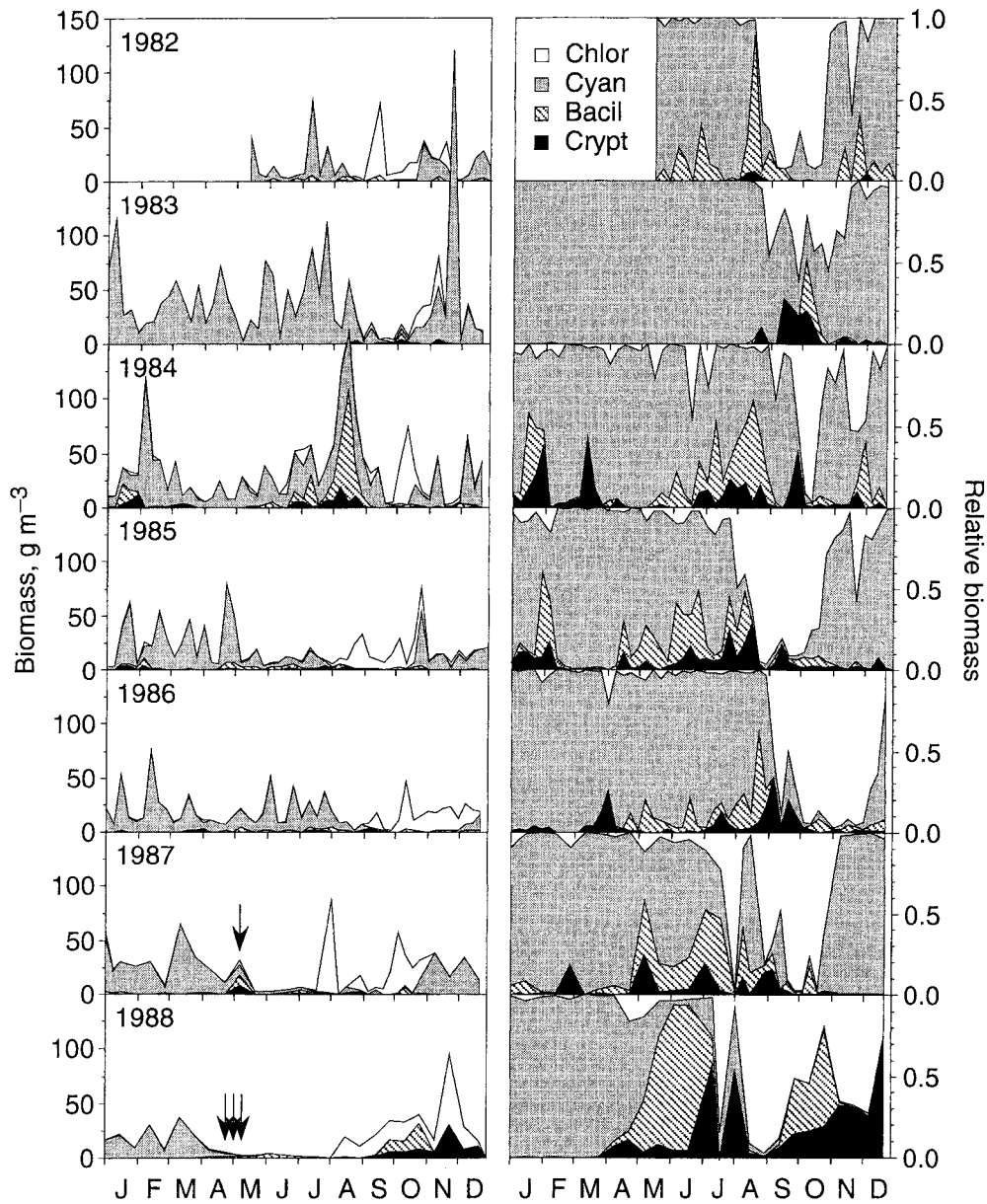


Fig. 1. Phytoplankton abundances and composition by principle taxonomic groups during 1982–1988 in Hartbeespoort Dam, RSA. Chlor = Chlorophyta; Cyan = Cyanobacteria; Bacil = Bacillariophyta; Crypt = Cryptophyta. Arrows denote flushing events when *Microcystis* scums were flushed downstream over the dam wall.

year the water column *Microcystis* standing crop declined abruptly, due to mass sinking to the bottom sediments (Zohary and Roberts 1989). This decline coincided with a suite of environmental changes in various physical attributes (increased solar radiation, temperature, and winds) that resulted in thermal stratification of the lake and a deepening of the euphotic zone ( $z_{eu}$ ) relative to the mixed zone ( $z_m$ ) (Fig. 2). During this turbulent period, the advantage accruing to *Microcystis* from buoyancy regulation was reduced, and other algal groups (diatoms, cryptophytes, and chlorophytes) gained predominance in the phytoplankton assemblage via a rapid species successional episode, aided by intense grazing by large-bodied cladocerans (*Daphnia* spp.) (Jarvis 1986;

Jarvis et al. 1988). This succession culminated with the return of *Microcystis* dominance by early summer (Fig. 3). Further species-specific details can be found in Zohary et al. (1996).

Although the classical factors generally considered important in phytoplankton dynamics, such as temperature and nutrient concentrations, obviously affected the phytoplankton of Hartbeespoort Dam, the abundance of *Microcystis* was clearly a dominating factor (Fig. 4). For example, the greens *Carteria cordiformis*, *Dictyosphaerium pulchellum*, *Pandorina* spp., and *Scenedesmus linearis* tended to increase across a broad spectrum of temperature and nutrient conditions, but only when *Microcystis* was rare. In contrast, other species

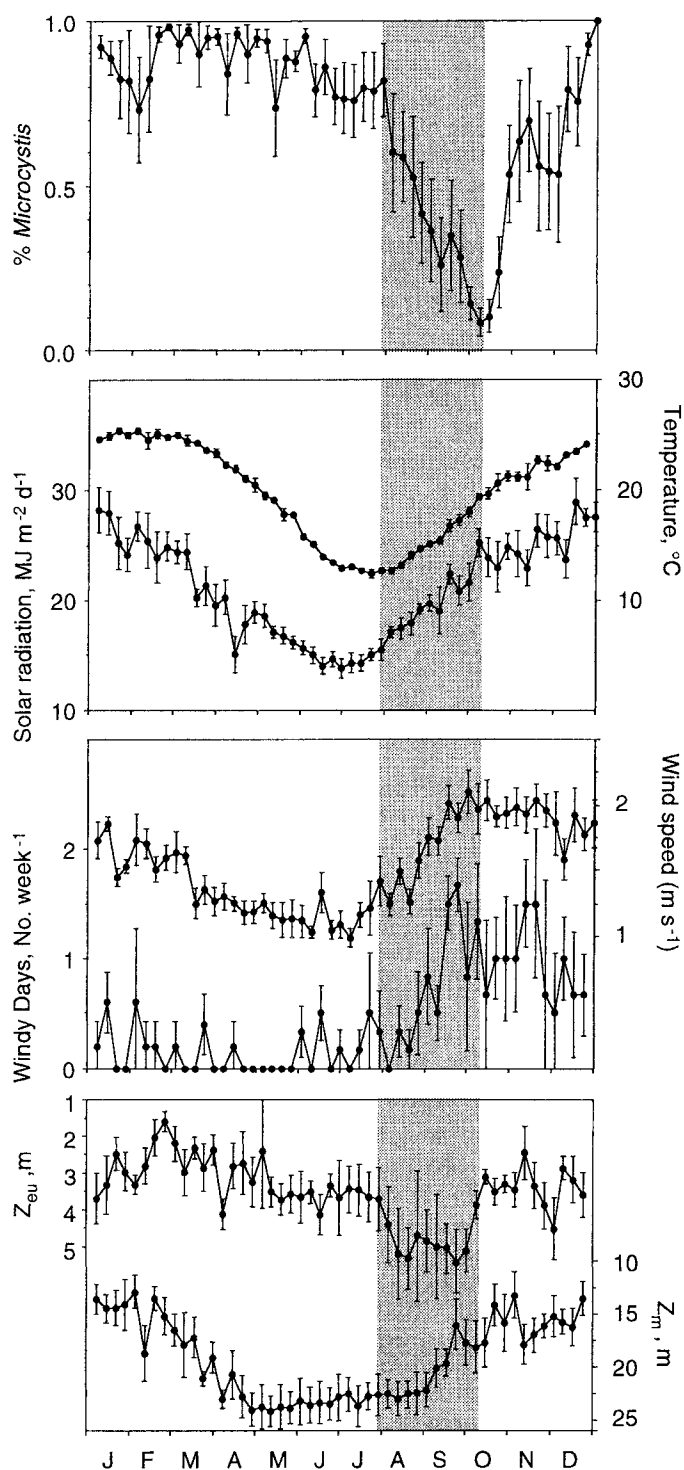


Fig. 2. Mean ( $\pm$ SE) annual pattern of *Microcystis* relative abundance (% of total phytoplankton biomass) and various physical attributes of Hartbeespoort Dam during 1982–1988. Windy days are the number of days per week in which wind speeds  $\geq 2.5$  m s<sup>-1</sup> occurred;  $z_m$  = depth in meters of upper mixed layer (epilimnion); and  $z_{eu}$  = depth of the euphotic zone (measured as the depth at which 1% of surface irradiation penetrated). The shaded area highlights the late winter–early spring decline of *Microcystis* dominance.

(the diatoms *Cyclotella meneghiniana* and *Melosira* (syn. *Aulacoseira*) *granulata* and the cryptophytes *Chroomonas* sp. and *Cryptomonas* sp.) demonstrated greater tolerance to (i.e., occurred more frequently with) high *Microcystis* abundances, even though they tended to proliferate mostly at lower *Microcystis* abundances.

The mechanism whereby *Microcystis* controlled growth in other species appears to be via its control over light penetration in the water column. Although several factors can affect light penetration in water (Kirk 1983), in Hartbeespoort Dam mean chlorophyll concentrations in the euphotic zone accounted for 63% of the variability in euphotic zone depth ( $z_{eu}$ ), (Fig. 5, upper panel). Hence, periods of *Microcystis* domination of the phytoplankton assemblage closely corresponded to periods of minimum  $z_{eu}$  (Fig. 5, lower panel). With the late winter–early spring collapse of *Microcystis* domination,  $z_{eu}$  increased with subsequent increases in species diversity (as indicated by  $H'$ ) (Fig. 6). As such, species diversity was positively correlated with  $z_{eu}$ .

*Increased disturbance*—The pattern of *Microcystis* domination during summer through winter and high species diversity in spring was persistent during 1982–1986. With the reduction in phosphorus inputs into the lake and repeated flushings of the *Microcystis* scums downstream, the dynamics of *Microcystis* domination destabilized after 1986. Subsequent to the enactment of the 1 mg L<sup>-1</sup> P standard for effluents in the Transvaal Highlands, the external loading of P to Hartbeespoort Dam gradually declined. This reduced P loading, concomitant with the refilling of the lake following 5 yr of drought, led to lower P concentrations and higher N:P ratios in the lake (Table 1), both important factors in *Microcystis* dominance (Reynolds and Walsby 1975). In 1987, a single hyperscum flushing event in May removed a large portion of the *Microcystis* biomass, though the population was able to recover by late spring (see Fig. 1). However, repeated flushings of the *Microcystis* scums in April–May 1988 removed most of the water column *Microcystis* biomass, and for the first summer since the *Microcystis* era began in the 1970s, *Microcystis* failed to bloom. The phytoplankton of Hartbeespoort Dam were dominated by cryptophytes and chlorophytes, and both species number and diversity were higher than during previous years (Fig. 7). This new non-*Microcystis*-dominated phytoplankton assemblage prevailed for 3 yr, although another nonbloom non-scum-forming cyanobacterium, *Aphanothece* sp., did dominate the phytoplankton assemblage during January–April 1990 (Chutter and Rossouw 1991). However, the situation did not persist into the 1990s; *Microcystis* returned to a level of dominance in 1991 similar to that observed for the 1980s (G. Quibell pers. comm.).

## Discussion

Since the 1961 publication of Hutchinson's "Paradox of the Plankton", there have been numerous studies directed toward explaining high phytoplankton species diversity in the seemingly homogeneous pelagia of lakes. If phytoplankton do indeed experience stable environmental conditions in lakes, then perhaps we underestimate the number of resour-

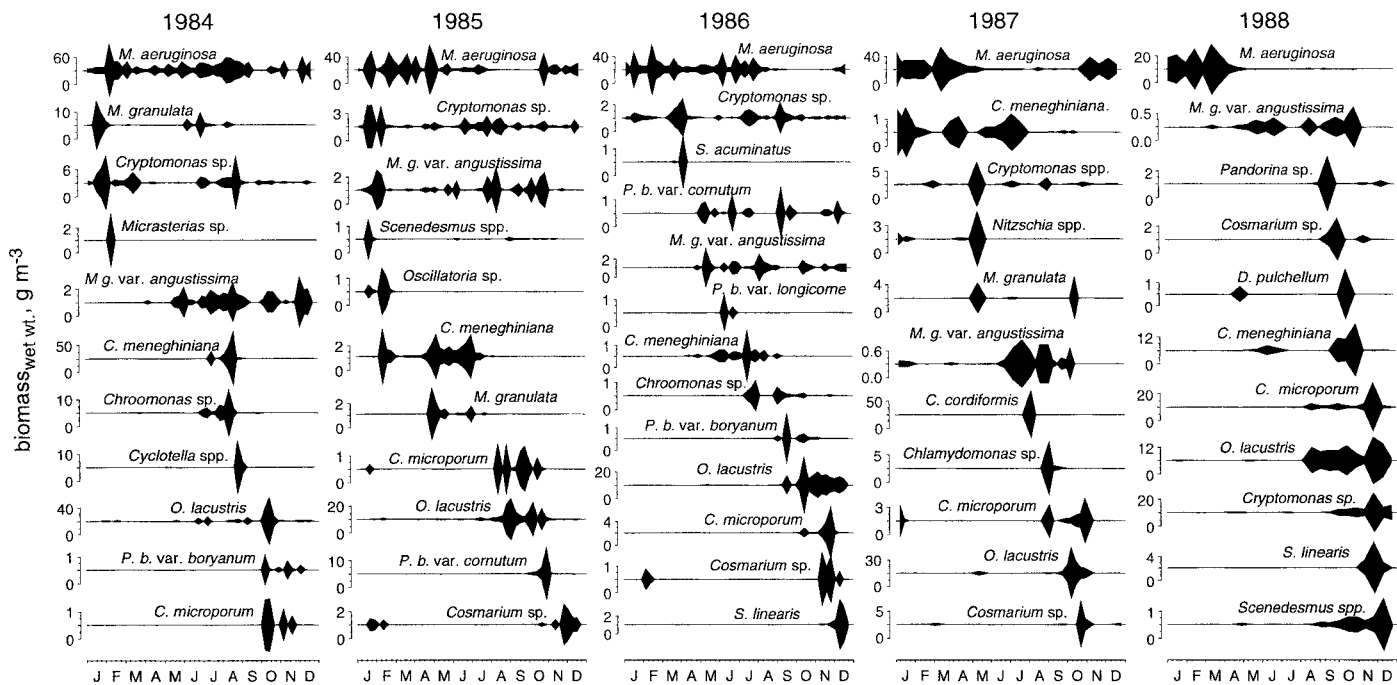


Fig. 3. Seasonal patterns in biomass of major phytoplankton taxa in Hartbeespoort Dam during 1984–1988. Species are ordered each year to approximate the major trends in species succession. Note different scales for each taxon.

es actually limiting phytoplankton growth. For example, Petersen (1975) suggested that nutrient uptake kinetics of individual phytoplankton taxa are different enough from one another to allow several taxa to exist simultaneously; each limited by a different nutrient or combination of nutrients. However, and in line with Hutchinson's initial speculation of environmental heterogeneity, many studies have shown that phytoplankton rarely experience large-scale (at the population level) stable environmental conditions, and that environmental changes at the scale of subpopulations can be too rapid for competitive exclusion to lead to stable, low-diversity assemblages (e.g., Richerson et al. 1970; Tilman et al. 1982; Reynolds 1988). Within the last decade, studies relating the intermediate disturbance hypothesis to high phytoplankton species diversity in freshwater and marine pelagia have focused on the role of environmental temporal heterogeneity relative to algal generation times (e.g., Reynolds 1988; Padišák 1992; Sommer 1995). Although there is evidence that competitive trends in phytoplankton can be equally rapid in both equilibrium and nonequilibrium conditions (Grover 1991a,b), it is widely held that both spatial and temporal heterogeneity in pelagic environments maintain nonequilibrium conditions, and therefore the competitive exclusion principle is not readily applicable to phytoplankton at the whole-lake scale.

In contrast, the hypertrophy and the subtropical climate with low wind speeds of Hartbeespoort Dam provided a suitable environment for the development each year of equilibrium, or at least near-equilibrium, conditions (especially with regard to the typically growth-limiting nutrients, N and P), such that competitive exclusion was a principle factor involved in phytoplankton dynamics (i.e., *Microcystis* often constituted >90% of the phytoplankton biomass). Nitrogen

and phosphorus were in excess of phytoplankton requirements throughout the year, and temperature never dropped below 12°C. As such, large blooms of buoyant phytoplankton (*Microcystis*) could develop in the upper waters to the point of creating conditions of light limitation for nonbuoyant taxa.

In Hartbeespoort Dam, the rate of primary production is strongly regulated by the underwater light regime (Robarts 1984; Robarts and Zohary 1984, 1987). Under conditions of light deprivation, algae that are capable of adjusting their position in the water column (via buoyancy or swimming behavior) can gain a competitive advantage over species that rely solely on water movements to overcome the force of gravity (Reynolds and Walsby 1975). Robarts and Zohary (1984) demonstrated experimentally that algal chlorophyll concentration was the major factor determining underwater light attenuation in Hartbeespoort Dam. Hence, as *Microcystis* abundance increased in summer and fall, light penetration was severely reduced, and  $z_{eu}$  decreased (see Fig. 5) such that nonbuoyant taxa were restricted to relatively shaded, darker waters. Interestingly, Robarts and Zohary (1984) also found that *Microcystis* colony size moderated the effect of chlorophyll concentration on light attenuation. As *Microcystis* accumulated at the surface, a concomitant increase in colony size for a given biomass decreased light attenuation relative to that with smaller colony sizes, thereby reducing population self-shading. They concluded that the double ecological advantage of buoyancy and increasing colony size with increasing abundance made *Microcystis* a formidable and successful competitor in the lake.

Even with the onset of winter, as solar radiation and temperatures declined to suboptimal levels for *Microcystis* (Robarts and Zohary 1987, 1992), the dense surface accumula-

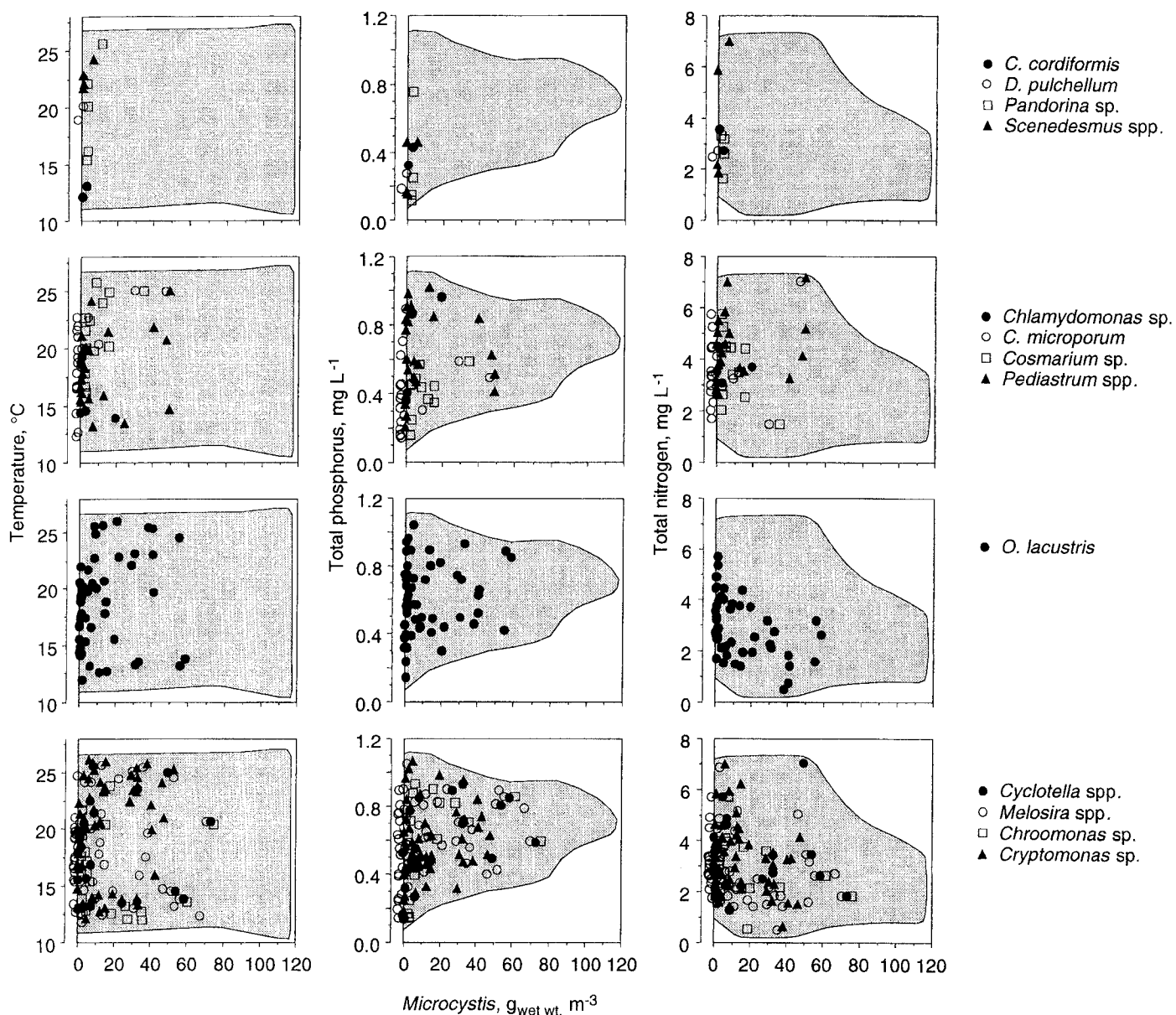


Fig. 4. Environmental conditions favoring net doubling of biomass for weekly (May 1982–December 1986) or biweekly (January 1987–December 1988) estimates of the standing populations of phytoplankton taxa in Hartbeespoort Dam. All taxa shown in Fig. 3, except *Micrasterias* sp. and *Oscillatoria* sp., which occurred only in 1984 and 1985 during the *Microcystis* period, and *Nitzschia* spp., *Pandorina* sp., and *D. pulchellum*, which occurred after the high-intensity disturbances of 1987 and 1988. Species complexes (*Scenedesmus* spp., *Melosira* spp., *Cyclotella* spp., and *Pediastrum* spp.) are represented as single taxa. Points indicate environmental conditions prevalent at times when biomass of indicated taxa doubled (i.e., when growth conditions were favorable). Shaded areas represent the range of conditions that existed during the study period. Species are ordered from top to bottom with increasing tolerance (i.e., increasing frequency of occurrence) to high *Microcystis* biomass. Open circles are shifted left and open squares right by the width of one point to improve clarity.

tions of *Microcystis* maintained control of the underwater light climate and the exclusion of other algal taxa. A major contributing factor was the characteristically low wind velocities during fall and winter, which enabled *Microcystis* to float and further shade other nonbuoyant species, even though *Microcystis* growth rates were diminished and much of the population was senescent (Zohary and Breen 1989). Only with the physical mixing of the upper water layers by the increased spring winds, which led to the breakup of the

surface scums, deeper mixing, and increased light penetration, could other taxa proliferate. However, because *Microcystis* can maintain a large stock population on the lake sediments following a bloom crash (Reynolds et al. 1981), and because N and P concentrations were always high in Hartbeespoort Dam, *Microcystis* was able to reestablish dominance following the return of favorable conditions and create a situation in which light again became the primary limiting resource. The combined effect of reduced ambient phospho-

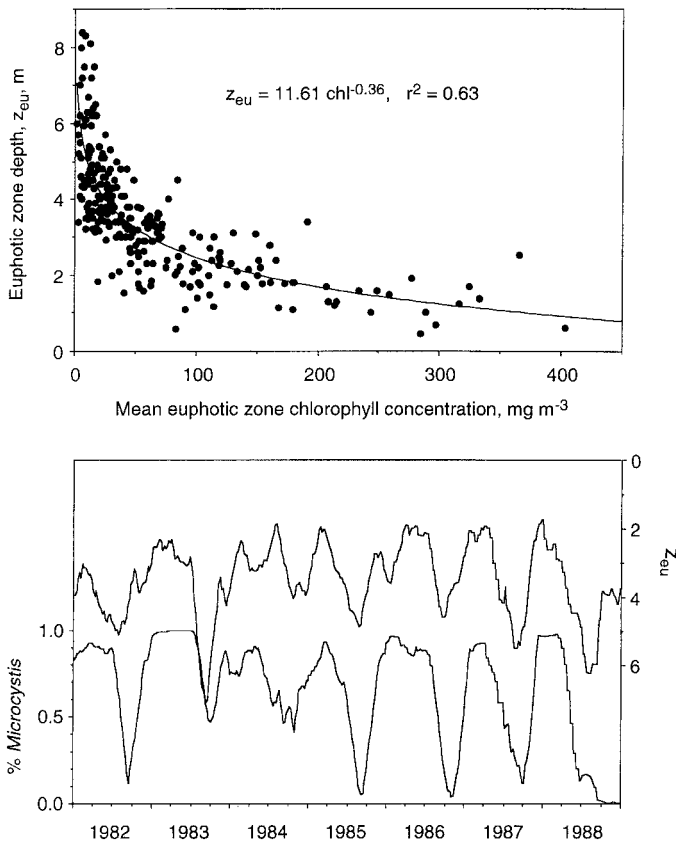


Fig. 5. Relationship between mean chlorophyll *a* concentrations ( $\text{mg m}^{-3}$ ) in the euphotic zone ( $z_{\text{eu}}$ ) and depth of  $z_{\text{eu}}$  (upper panel) and temporal changes in  $z_{\text{eu}}$  and relative *Microcystis* biomass (running averages of 5 sampling days used to improve clarity) (lower panel) in Hartbeespoort Dam during 1982–1988.

rus concentrations, increased N:P ratios, and intentional flushing of *Microcystis* scums from the lake prevented the reestablishment of *Microcystis* dominance in late 1987 and in 1988.

Phytoplankton development proceeded in Hartbeespoort Dam in accordance with one of three scenarios: domination by *Microcystis* and exclusion of other taxa, short-term (seasonal) loss of *Microcystis* dominance and proliferation of other taxa, and long-term (multi-annual) loss of *Microcystis* dominance and proliferation of other taxa. We interpret these dynamics in terms of competitive exclusion and disturbance. *Microcystis* dominance of the phytoplankton community in a system with one primary limiting resource (light) typifies predictions of the competitive exclusion principle (Hardin 1960). The disruption of the *Microcystis*-dominated community, followed by rapid species succession, increased diversity, and eventual reestablishment of *Microcystis* dominance typifies expectations from IDH (Connell 1978). Contrary to IDH, increased intensity of disturbance to *Microcystis* (in the form of lake flushing) yielded a similar response in species diversity by the phytoplankton community. Based on these patterns observed in Hartbeespoort Dam, we define and qualify three realms of disturbance intensity relative to resistance (defined as the ability of the community to oppose change) and resilience (defined as the

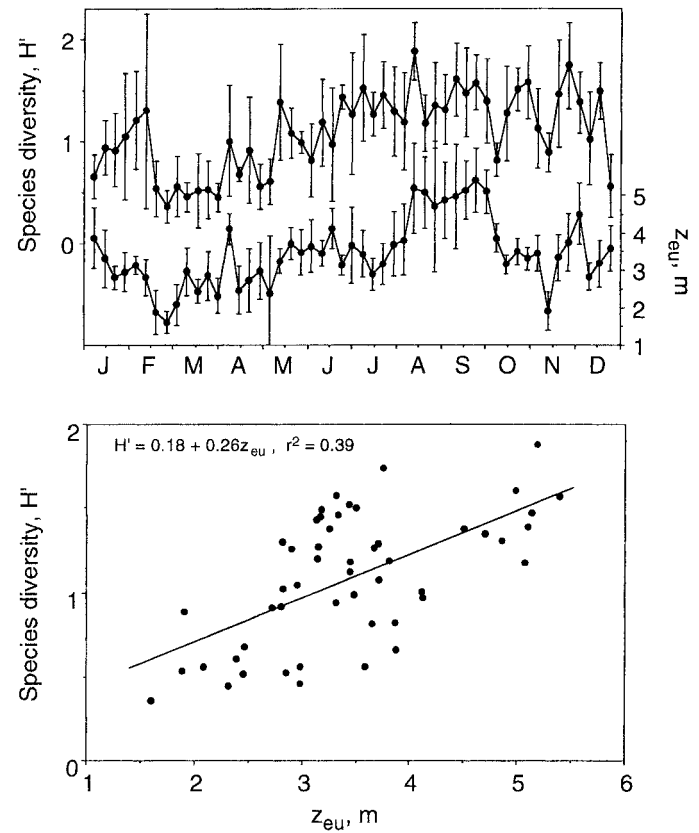


Fig. 6. Mean ( $\pm$ SE) annual pattern in phytoplankton species diversity ( $H'$ ) and euphotic zone depth ( $z_{\text{eu}}$ ) (upper panel) and linear relationship between the two variables (lower panel) in Hartbeespoort Dam during 1984–1987.

ability of the community to return to predisturbance conditions) to disturbance (defined as an event that causes change in a community; but see Reynolds 1997 for discussion of “intensity of forcing” versus “disturbance”): (1) no or slight disturbance below the levels of resistance and resilience; (2) intermediate intensity disturbance, which can overcome the resistance to that disturbance, but resilience remains high; and (3) higher intensity of disturbance, which also overcomes resistance but is accompanied by a reduction in resilience to that disturbance (Fig. 8). For this demonstration, we quantified resistance as mean epilimnetic water temperature, based on Thomas and Walsby’s (1986) finding that *Microcystis* buoyancy regulation is severely impaired at low winter temperatures, and on the general notion that growth in *Microcystis* is temperature dependent (Robarts and Zohary 1987). Resilience was approximated by an index of water column P concentrations and estimated “overwintering seed stock” of *Microcystis* in spring, where the seed stock was assumed proportional to the maximum *Microcystis* biomass prior to the bloom crash. Disturbance by mixing was approximated as mean weekly wind speed, while disturbance by flushing was arbitrarily allocated values of 2 in May 1987 and 4 in April–May 1988.

Figure 8 demonstrates that the typical seasonal collapse of the *Microcystis* bloom and increased species diversity occurred when a disturbance was applied sufficient in strength

Table 1. Mean lake surface area (SA) and loading rates and water column concentrations of total nitrogen (TN) and total phosphorus (TP) for Hartbeespoort Dam for the hydrological years 1982–1990 as reported by Chutter (1989) and Chutter and Rossouw (1991).

Hydrological year	Maximum depth (m)	Surface area (km <sup>2</sup> )	Areal loading rate			Water column concentration		
			TP (g m <sup>-2</sup> yr <sup>-2</sup> )	TN (g m <sup>-2</sup> yr <sup>-1</sup> )	TN:TP (wt:wt)	TP (μg L <sup>-1</sup> )	TN (mg L <sup>-1</sup> )	TN:TP (wt:wt)
1982–1983	26.6	10.2	20.6	76	4	668	3.4	5
1983–1984	25.4	8.9	25.9	102	4	750	2.3	3
1984–1985	25.8	9.5	20.2	97	5	666	2.6	4
1985–1986	25.7	9.3	18.6	141	8	505	4.8	10
*1986–1987	30.9	13.7	17.4	164	9	508	5.0	10
1987–1988	32.5	18.7	12.2	114	9	327	3.3	10
1988–1989	32.7	19	9	88	10	140	2.4	17
1989–1990					10	134	2.8	21
Average (1982–1986)	25.9	9.5	21.3	104	5	647	3.3	5
Average (1987–1989)	32.0	18.9	10.6	101	10	234	2.9	13.5
% change	24	98	-50	0	90	-64	-12	146

\*The 1986–1987 hydrological year is considered transitional and not included in calculations of multiannual averages.

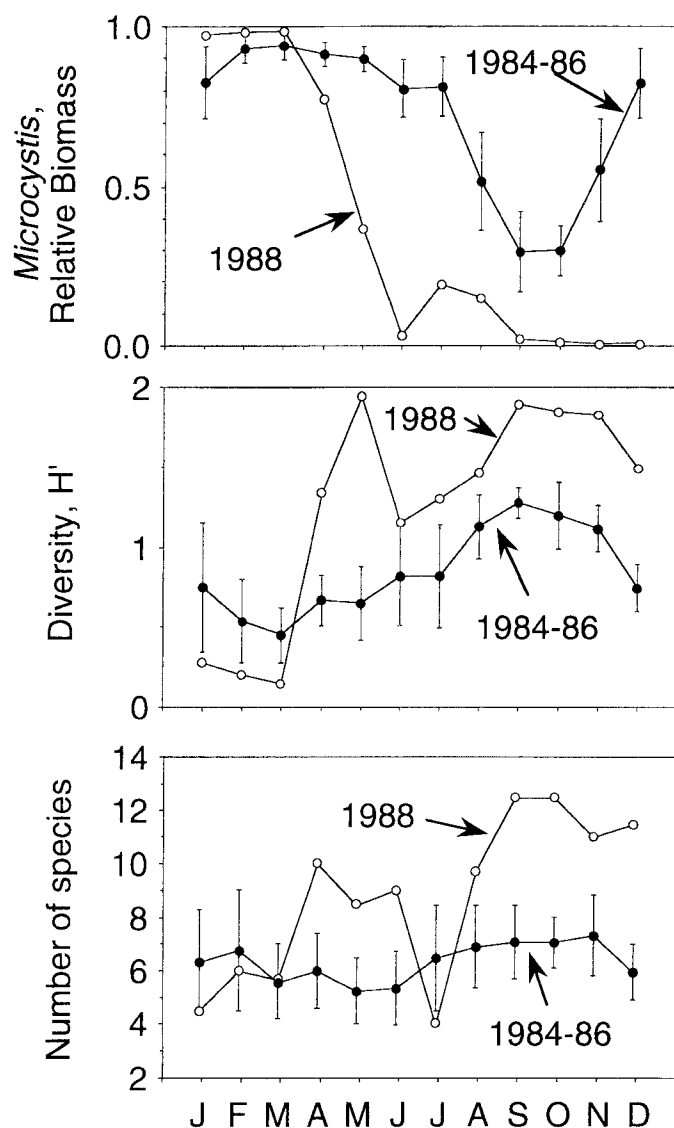


Fig. 7. Comparison of monthly mean relative biomass of *Microcystis*, Shannon's  $H'$ , and number of phytoplankton species during 1988 with the multi-annual monthly ( $\pm$ SE) means for the period 1984–1986.

to overcome *Microcystis*'s resistance to mixing. Typically, the disturbance by wind began when resistance to mixing was relatively low. Because P concentrations in Hartbeespoort Dam were always in excess during 1982–1986, and a large proportion of the *Microcystis* biomass accumulated each year in the lake was “stored” on the lake bottom following the bloom crash, resilience to the wind-induced stress was always relatively high. Hence, *Microcystis* generally returned to its previous levels of domination as the intensity of disturbance declined and resistance to mixing increased. In May 1987, the first attempt of flushing *Microcystis* surface scums downstream led to similar seasonal events in the phytoplankton community (collapse of the *Microcystis* bloom and increased species diversity), though the timing is considerably earlier in the year, occurring when resistance was high. Resilience to this flushing event was also high, as

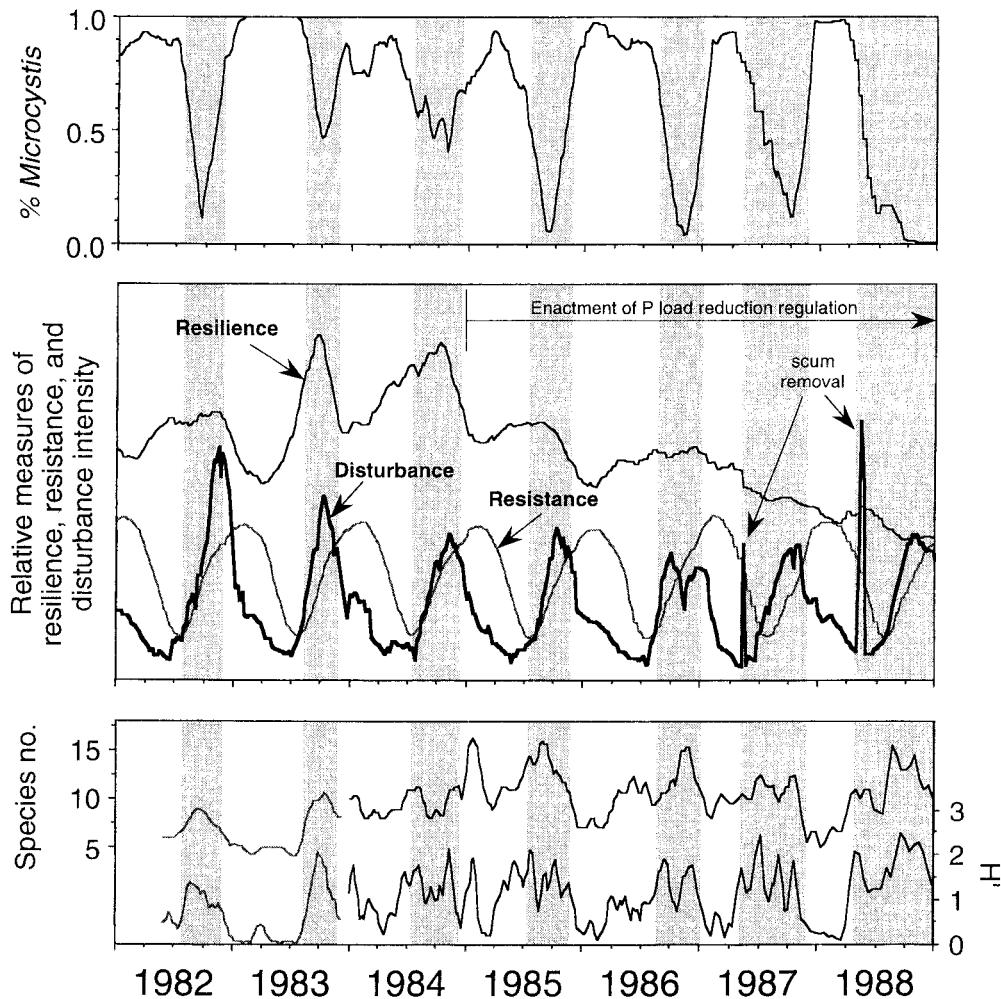


Fig. 8. Multi-annual pattern in relative *Microcystis* abundance (upper panel); schematic diagram depicting hypothesized relationships between disturbance intensity, resistance to wind-induced mixing stress, and resilience to disturbance (center panel); and multi-annual patterns in species number and  $H'$  (lower panel). Disturbance intensity was quantified as a sum of wind speed and flushing intensity, where flushing intensity was set arbitrarily at 0 for no flushing, 2 for the single flushing event of 1987, and 4 for the multiple flushing events in 1988; resistance as mean epilimnetic water temperatures; and resilience as a product of water column P concentrations and summer maximum *Microcystis* standing stock each year (as a proxy for the potential inoculum from the lake sediments for the subsequent summer bloom). For simplicity all units for these indices were omitted. Species number and  $H'$  in 1982 and 1983 were based on phytoplankton counts using different methodology (see text) and are shown here for relative comparison of annual patterns only.

only a fraction of the population was flushed downstream and P concentrations were still high. The second flushing event (in April–May 1998) also occurred at a time when resistance in the *Microcystis* population was high. However, this time the disturbance was much greater in intensity and at a time with relatively low resilience. Nevertheless, species diversity following the second flushing disturbance was similar to that following the previous intermediate intensity disturbances (seasonal mixing and first flushing), except that the period of high diversity was protracted. Neither nutrient concentrations nor the initial spring seed stock of *Microcystis* was sufficient to guarantee the return of *Microcystis* dominance to the Hartbeespoort Dam phytoplankton for 3 yr. However, with time *Microcystis* proliferated, and by summer

1991 *Microcystis* became the dominate member of the Hartbeespoort Dam phytoplankton once again (G. Quibell pers. comm.). This return of *Microcystis* suggests that the disturbances of 1988 were not strong enough to cause *Microcystis*'s extinction from the system in the long term. The use of temperature and nutrients as measures of resistance and resilience by *Microcystis* to wind-induced mixing stress in Fig. 8 is primarily illustrative, as many factors will undoubtedly be involved. However, the correspondence among these factors is remarkably close. Clearly, in order to determine precise relationships between environmental disturbances and community organization, both resistance and resilience, in addition to the disturbance itself, must be quantified.

Recently, some debate has arisen regarding the applica-

bility of the IDH to plankton communities (Wilson 1990, 1994; Padišák 1994). Most of the arguments have focused on two integral components of the IDH: the definition of disturbance and the scale at which a disturbance interacts with a plankton assemblage. A problem of semantics appears to underlie these arguments. Criticism directed at problems associated with defining and quantifying external environmental disturbances in planktonic systems is similar to that for other aquatic and terrestrial systems. A major weakness of the IDH often pointed out is that a disturbance is usually defined or characterized by the response evoked in the populations under study, rather than by independent attributes of the disturbance itself (see Sousa 1984). As such, the analysis of a given disturbance takes on a rather tautological nature (Rykiel 1985). Tautology notwithstanding, the relationship between an external disturbance and an affected ecological system is unique, dependent on both the strength of the disturbance and the resistance and resilience of the biotic system. That uniqueness dictates that the disturbance can only be measured in terms of the changes evoked in that system (Pickett and White 1985). Nevertheless, Sommer's (1993) quantification of the effects of wind-induced disturbance on phytoplankton community structure in two north-temperate lakes does suggest that independent measures of disturbance are possible.

With regard to Hartbeespoort Dam, we too are faced with the ever-present problem of "quantification of the disturbance." Granted, although we have identified wind-induced mixing and physical removal of *Microcystis* scums as the disturbances to *Microcystis* domination, we too define the intensity of disturbance based on the elicited response in the phytoplankton, but with consideration of the relative degrees of resistance and resilience to that disturbance. However, we feel confident that we have correctly identified the response-disturbance link, and a lack of independent quantification of disturbance intensity does not detract from our conclusion that the noted disturbances were key factors in driving the phytoplankton dynamics of Hartbeespoort Dam. Nevertheless, we are faced with a challenge to the direct translation of Connell's IDH to the Hartbeespoort Dam phytoplankton. All disturbances elicited similar responses in both species diversity and species number (see Fig. 8) suggesting one of three conclusions: the disturbances are located on either side of the nodal point of Connell's diversity-disturbance relationship (Fig. 9A), the disturbances are similar (Fig. 9B), or the node in Connell's relationship should be expanded into a plateau (Fig. 9C). Unfortunately, we are presently unable to offer a definitive suggestion for which of the three interpretations is correct. The first option seems unlikely, though it could be argued that the second option is tenable. From the viewpoint of all other phytoplankton taxa, both disturbances yielded the same result—the demise of *Microcystis* and increased light availability. However, we speculate that Fig. 9C represents the more likely interpretation of our results, as the two disturbances were fundamentally different in the nature by which they affected the ecosystem. Nevertheless, in either of the three interpretations, the differences in duration of high diversity noted after each of the disturbance intensities suggest a modification of Connell's original relationship to include a time component during which in-

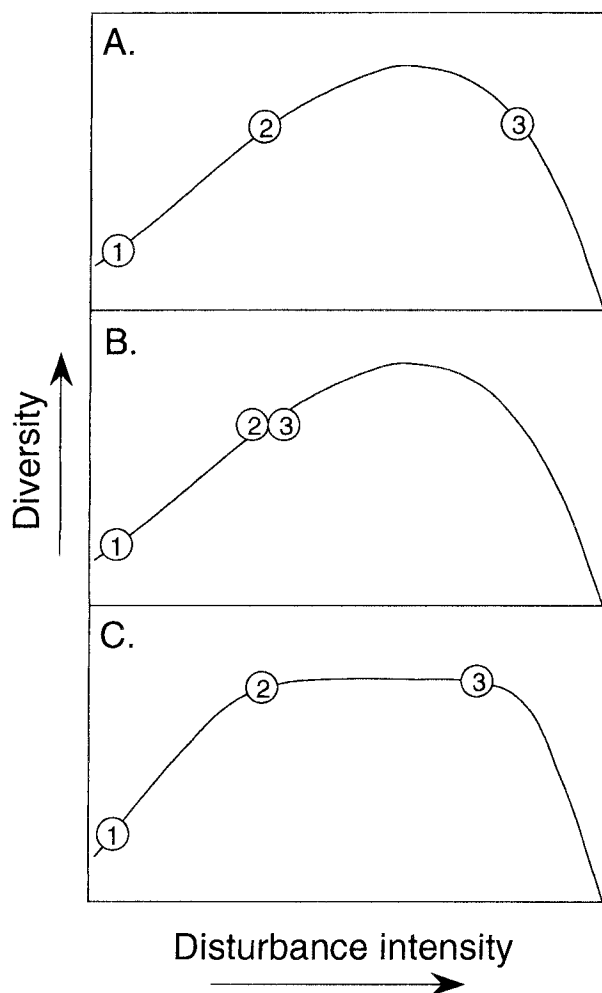


Fig. 9. A and B: Hypothesized positions of intensities of disturbances in Hartbeespoort Dam along Connell's (1978) disturbance-diversity relationship. Numbers refer to (1) no disturbance; (2) seasonal wind-induced mixing stress and single flushing of *Microcystis* surface scums downstream in 1987; and (3) repeated flushing of *Microcystis* surface scums in 1988. C: Same as A and B, except Connell's relationship is modified to include a broad plateau over a range of intermediate disturbances in which a similar response in diversity is elicited.

creased diversity is maintained following a given disturbance (Fig. 10). Thus, severe intensity disturbances may not necessarily yield higher or lower levels of diversity compared with moderate-intensity disturbances. Rather, the period of nonequilibrium, and hence increased diversity, may be longer with the larger disturbance. Obviously, at some point on the disturbance continuum, diversity will drop precipitously as species are removed (via extinction) by the disturbance (Connell 1978).

Regarding phytoplankton assemblages specifically, Wilson (1990, 1994) has argued that disturbances in phytoplankton analogous to terrestrial systems simply do not occur. Based on the assertion that algal generation times are measured in terms of hours to days, Wilson contends that the typically postulated disturbances (e.g., fluctuations in nutrient supply, sudden storms, periods of strong winds; Padišák

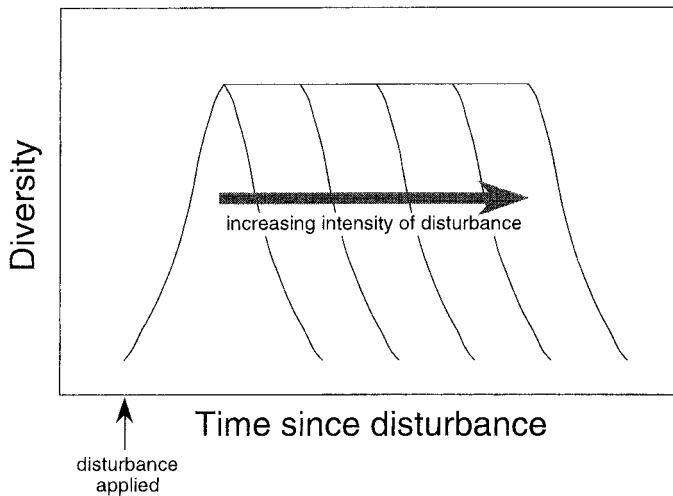


Fig. 10. Schematic representation of the effect of disturbance intensity (relative to resistance and resilience to that disturbance) on duration of the consequent increased diversity.

1994) are equivalent to climate change events lasting tens to hundreds of years in terrestrial analogs. Therefore, he suggests that gradual climate change (*sensu* Huston 1979) is a more appropriate hypothesis to explain high species diversity in phytoplankton assemblages. Wilson's problem with defining the appropriate scale is apparently centered on a misconception of heterogeneity in pelagic environments, as he stresses that "for IDH to operate, it [the disturbance] must be *patch* disturbance" (1994, p. 180). Moreover, he states that few disturbances like storms could operate on the scale of phytoplankton patches (Wilson 1994, p. 180). It is apparent from such arguments that the IDH most often evokes images of tree-fall gaps and other small-scale species voids created by local physical disturbances. However, as clearly detailed in Connell's (1978) original formulation, the IDH can include a variety of disturbances in both time and space (Reynolds 1994, 1997). Moreover, the temporal and spatial scales within which disturbances have been implicated are based soundly in both theoretical and experimental descriptions of hydrodynamic properties of pelagic environments. We can only conclude, therefore, that given a proper understanding of spatial and temporal heterogeneity in pelagic environments (e.g., Richerson et al. 1970), arguments pivoting around relative scales of patches and disturbances would cease.

It is interesting, and perhaps fortuitous, that the scale problem perceived by Wilson (1994) does not apply in the case of Hartbeespoort Dam. Here, the entire pelagic system was stable, with equilibrium conditions prevailing much of the year. The disturbances of interest were those that disrupted *Microcystis* dominance of the underwater light regime. As such, the temporal scale of the disturbances is directly analogous to those commonly noted in terrestrial systems, i.e., at the level of months to years. Moreover, there were only two primary patches between which *Microcystis* migration could occur. Most of the population existed in the water column patch for 6–10 months each year. However, following each intermediate disturbance event, the sediment

patch provided the source of invading *Microcystis* to the water column each spring. The essence of the intense disturbances in 1987–1988 was the reduction in size of this invading patch via repeated flushing of the *Microcystis* downstream.

Perhaps one of the more difficult aspects of addressing the question "What maintains high phytoplankton species diversity?" is where and when we choose to ask. Our analysis of Hartbeespoort Dam phytoplankton demonstrates that a pelagic environment with high diversity is not necessarily the best place to start. There is clearly a benefit in beginning with a system of low diversity with a single dominant taxon and watching that system as that dominant taxon responds to a disturbance. Unfortunately, by using a seasonal to annual timescale, we are unable to address the timescale phenomena postulated by Reynolds (1988) and others (*see* Padisák et al. 1993) with regard to maintenance of high phytoplankton diversity (i.e., algal generation times). Nevertheless, we do not exclude the possibility of other disturbances operating at smaller temporal scales during the brief spring period of high diversity. For example, the spring increase in zooplankton grazing pressure (Jarvis 1986) could be a driving factor in the rapid species succession (Padisák 1992). Indeed, we would also suggest that smaller scale disturbance events were involved in allowing the cryptophytes and diatoms to coexist with *Microcystis* on occasion (*see* Figs. 3, 4). We can also suggest, however, that perhaps the hypertrophic status of Hartbeespoort Dam diminished the role of heterogeneity such that a common resource (in this case light) could often be limiting simultaneously in all patches (*sensu* Petersen 1975).

Equilibrium conditions in communities are rarely achieved in nature because temporal and spatial variability within both communities and their environments interact dynamically (Sousa 1984). If this interaction results in repetitive and predictable changes in community structure, we might label the change as seasonal. At other times, the interaction between communities and their environments end in less readily predictable results, and we arbitrarily define the interaction as a disturbance. Although the yearly disruption of *Microcystis* dominance in Hartbeespoort Dam was seasonally predictable, we view it as a disturbance because the *Microcystis* population within the surface waters of Hartbeespoort Dam was physically mixed down into the water column by the action of wind. Without this breakup of the *Microcystis* layer in the upper water column, the underwater light climate would have continued to prevent other species from proliferating. Regardless of the subtlety in semantics and the scale at which a community is examined, disturbances at some level by some agent seem to be ubiquitously involved in species, population, assemblage, and community dynamics (Sousa 1984; Pickett and White 1985; Pickett et al. 1989).

Identification and understanding of factors underlying patterns in species abundances in nature continues to be a central issue in ecology. As the list of these factors is virtually endless, broadly applicable rules are sought (May 1986). The IDH is one such generalization that fosters growing support (e.g., *see* reviews Sousa 1984; Petraitis et al. 1989; Caswell and Cohen 1993). Although we have not provided an actual

test of the IDH, we have provided further evidence that indeed IDH is broadly applicable in ecology, and its utility in understanding community structure and species dynamics in nature, in particular, phytoplankton species succession, is undeniable.

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