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Disturbance-diversity relationships in two lakes of similar nutrient chemistry but contrasting disturbance regimes

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Abstract

Phytoplankton diversity was studied in two North German lakes of comparable nutrient chemistry but different exposure to winds. In both lakes, phytoplankton was primarily N-limited but diatoms were Si-limited. Pluβsee had a very constant mixing depth during summer, while week-to-week changes of several meters were quite common in the more exposed Behler See. In Pluβsee, phytoplankton biomass during summer came closer to the carrying capacity as defined by the available total N. In Pluβsee there was a marked decline of diversity during the summer maximum of biomass, while this decline was less pronounced in Behler See. It is concluded that disturbances which prevented phytoplankton from reaching the carrying capacity also maintained a high level of diversity. A negative response of diversity to undisturbed conditions became apparent, after phytoplankton biomass had exceeded about 5% of the carrying capacity.

Introduction

Attempts to explain the coexistence of phytoplankton species and the avoidance of 'competitive exclusion' (i.e. attempts to solve Hutchinson's 'paradox of the plankton', 1961) fall into two categories: The equilibrium theory of competition (Petersen, 1975; Tilman, 1982) predicts that different species can coexist by being limited by different resources. Disequilibrium approaches (Richerson *et al.*, 1970; Grenney, 1973; Armstrong & McGehee, 1976; Levins, 1979; Ebenhöh, 1988; Grover, 1990) predict that environmental variability permits the coexistence of species competing for the same resource. Both hypotheses are by no means mutually exclusive and might be additive in their potential contribution to 'solve Hutchinson's paradox'. Culture experiments have supported both: Experiments with undisturbed continuous cultures (e.g. Tilman, 1977; Sommer, 1983) have supported the first prediction; experiments with discontinuous nutrient supply (e.g. Turpin & Harrison, 1980; Robinson & Sandgren, 1983; Sommer, 1984, 1985; Gaedeke & Sommer, 1986; Grover, 1988, 1989, 1991) have supported the second. The experiments by Gaedeke & Sommer (1986) have moreover supported Connell's (1978) 'intermediate disturbance hypothesis' by finding a diversity peak at disturbance intervals of *ca.* 3 generation times. Both frequent (intervals <1 generation time) disturbances of low intensity and rare but strong disturbances lead to low diversity levels.

Obviously, both resource partitioning and disturbance at the appropriate scale can increase the number of coexisting species and diversity. Therefore, comparative field studies with the purpose of testing the intermediate disturbance

hypothesis have to be carefully designed to avoid the influence of different numbers of limiting resources. In this study, I attempted to solve this problem by selecting two lakes which are similar in their nutrient chemistry (same number of limiting resources) but dissimilar in their exposure to wind (external disturbance).

Methods

The two lakes (Pluβsee and Behler See) were sampled during the vegetation period of 1990. For Pluβsee also data from another study in 1989 were also available (Sommer, 1991b).

Mixed phytoplankton samples were taken at weekly intervals from the epilimnion of both lakes and fixed with Lugol's iodine. Phytoplankton was counted according to the Utermöhl standard technique. At least 800 individuals were counted per magnification. Dissolved nutrients (soluble reactive phosphorus, nitrate, nitrite, ammonium, dissolved silicate) were measured according to standard techniques. The particulate fractions of biogenic elements were measured on filters: Carbon and nitrogen were measured in a CN-analyser (Carlo-Erba) after filtration onto glass-fiber filters, particulate Si after filtration onto Nuclepore filters, and particulate P after filtration onto cellulose-nitrate membrane filters. For more details on the chemical methodology see Sommer (1991a, 1991b).

The diversity of phytoplankton was calculated using a biomass-related version of Shannon's H' (for a comparison of diversity indices see Washington, 1984):

$$H' = - \sum p_i \times \log_2 p_i$$

where p_i is the relative importance of species i, here expressed by biomass (B_i/B_{tot}). Because of the low efficiency of the Utermöhl technique in counting picoplankton ($< 2 \ \mu m$) and because of the difficulties in their species identification, picoplankton were neglected. H' is thus a partial diversity covering phytoplankton $> 2 \ \mu m$.

Measurement of disturbance was more prob-lematic, because natural phytoplankton is subject to different kinds of disturbances which are scarcely comensurable. There is no generally acceptable common scale for changes in physical conditions, in nutrient supply, or in grazing pressure. Therefore, a biotic response variable was sought by which the impact of disturbance could be measured. This variable should be mathematically unrelated to diversity, otherwise the analysis of disturbance-diversity relationships would have become tautological. Here I chose the ratio between phytoplankton biomass (B) and the potential maximal biomass ('carrying capacity' in the classic sense, K). A similar approach, using a slightly different terminology, has been suggested by Reynolds (1991). By implication, disturbance is defined as any factor which prevents phytoplankton biomass from reaching K. This is a broad definition of 'disturbance' which includes physical (e.g. mixing events) and biotic factors (e.g. grazing). A maximum estimate of K was obtained from the total (dissolved plus particulate) fraction of the limiting nutrient. It was assumed that K is reached, when all of the limiting nutrient is incorporated into phytoplankton biomass and as much as possible biomass is made of it. This happens if the cell quota (Droop, 1973) is minimal (q_0). Since nitrogen is the primary limiting nutrient in both lakes, the estimate of K was based on N. A series of field studies in North german lakes (Sommer, 1991a, 1991b) had yielded the following estimate for natural populations:

$$q_0 = 0.037(\pm 0.14; S.D.) molN/molC.$$

The upper boundary of K (in mol C) was therefore estimated as 27 N_{tot}. To calculate the quotient B/K, biovolume was converted into carbon according to Rocha & Duncan (1985).

Results and discussion

Physical and chemical conditions

Pluβsee and Behler See were selected for this study because of their similarity in nutrient chem-

istry and their dissimilarity in exposure to wind and thus external disturbances. Both lakes are situated in the vicinity of Plön and are only 3 km apart. Pluβsee is much smaller (0.14 km^2) and strongly sheltered by surrounding moraine hills. Behler See (3.3 km^2) has a bigger wind fetch and is less sheltered. Due to their close vicinity they are subject to the same general weather conditions but the impact of wind events should be stronger on Behler See. Thus they are subject to the same frequency, but different intensities of external disturbances. This difference is clearly reflected in the stratification regime (Fig. 1).

Behler See (sampled weekly from March to September 1990) stratified later in the spring and started to circulate much earlier in autumn. The mixing depth (z_m) during the spring and summer stratified period was highly variable with minima of ca. 2.5 m and maxima of ca. 7 m. Week-to-week differences of ca. 4 m were quite common. Pluβsee (sampled weekly from February to early December 1989 and from March 1990 to December 1990) stratified nearly 2 months earlier and started to circulate 2 months later. The mixing depth during spring and summer never exceeded 5 m; week-to-week differences in spring and summer were usually small and never exceeded 1.5 m. The differences between 1989 and 1990 were minor with the notable exception that summerly mixing conditions ($z_m < 5$ m) persisted about half a month longer in 1989.
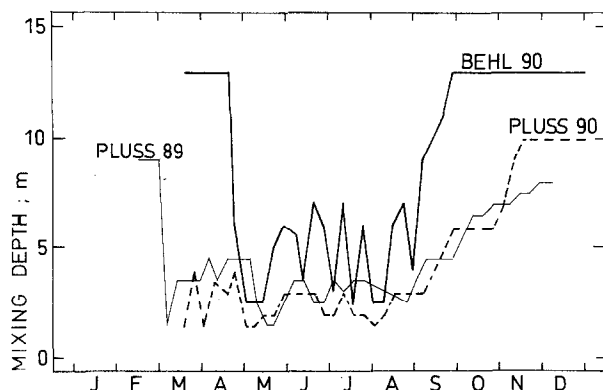

Fig. 1. Mixing depth of Behler See (1990) and Pluβsee (1989 and 1990). Values are truncated at the mean depth (13 m in Behler See and 10 m in Pluβsee).

Given that wind-induced mixing events during the stratified period can be major disturbances for phytoplankton succession (Reynolds, 1984, 1988) differences in the seasonal pattern of diversity between both lakes should be expected.

It was important for the selection of lakes that the same number of resources should become limiting during algal growth. Otherwise, differences in diversity indices would have been expected even under identical disturbance regimes (Tilman, 1982). A previous study on Pluβsee (Sommer, 1991b) had identified nitrogen and silicon (only for diatoms), but not phosphorus, as limiting nutrients by physiological methods (bioassays and measurements of cell quotas). Both lakes are quite similar in N and P availability. Total nitrogen concentrations before the start of the growing season were 40 μM in Pluβsee and 48 μM in Behler See, respectively. Total P concentrations at that time were 6.4 μM in Pluβsee and 5.6 μM in Behler See. During the entire study period TN:TP ratios were < 12; the same holds true for the ratio soluble reactive phosphorus:dissolved inorganic nitrogen ($NO_3 + NO_2 + NH_4$). Particulate C:N ratios of ca. 20:1 during the periods of maximal biomass in both lakes clearly suggest N-limitation; at the same time, N:P ratios in the particulate matter are < 15:1 (Goldman et al., 1979; Sommer, 1989, 1991a, 1991b).

Unlike to N and P, there are great differences in the Si availability between both lakes. Before the onset of algal growth the concentrations of dissolved Si were only 25 μM in Pluβsee but 106 μM in Behler See. In both lakes they fall to strongly limiting levels during the spring maximum of diatoms (2 μM in Behler See; 0.2 μM in Pluβsee) and stay limiting for diatom growth during the entire summer period (< 12 μM in Behler See; < 5 μM in Pluβsee).

Thus, the same three essential resources may become limiting in both lakes: nitrogen, silicate (for diatoms) and probably also light. If the lakes were chemostats, an equilibrium coexistence of three phytoplankton species could be anticipated in each case.

The response of phytoplankton

The total phytoplankton biomass showed a bimodal seasonal pattern in either lake (Fig. 2). The spring-bloom started already before the onset of stratification and continued into the stratified period. In mid-May, there was a marked minimum of phytoplankton biomass in spite of nearly optimal growth conditions; e.g. high nutrient availability, long daylength, high irradiance. Such mid-season minima under otherwise good growth conditions are termed 'clear-water phases' and can be explained by excessive zooplankton grazing (Lampert, 1988). After the clear-water phase, there was an extended summer maximum of biomass which is a characteristic feature for eutrophic lakes (Sommer *et al.*, 1986). Despite a very similar trophic status of both lakes, maximal summer biomasses were $1^{1}/_{2}$ to 2 orders of magnitude higher in Pluβsee than in Behler See; carrying capacities calculated from total nitrogen concentration were quite similar in both lakes, however. The carrying capacity was reached only in Pluβsee, during summer 1989; in summer 1990, the greatest attainment was 37% and, in Behler See, maximally 22%.

If resolved to the species level, the seasonal successions of phytoplankton in both lakes were quite different. However, if aggregated at a higher level of taxa (Fig. 3) and of functional groups (small, edible flagellates; large, inedible flagellates; small, edible immotile algae; large, immotile algae) the patterns were more similar and corresponded relatively well to the eutrophic standard model proposed by the plankton ecology group (Sommer *et al.*, 1986). The spring-bloom consists mainly of diatoms (*Stepanodiscus* spp. and *Asterionella formosa* Hass. in Pluβsee; *Aulacoseira islandica* Simonsen, *Stepanodiscus* spp. and *Asterionella formosa* in Behler See) and Cryptophycean flagellates, which tend to become more important with the onset of stratification. After the clear-water phase phytoplankton species which are resistant against grazing became dominant, first colonial green algae (e.g. *Pandorina*, *Sphaerocystis*), the colonial Cyanophyta (mainly *Anabaena*, but also *Microcystis*) and dinoflagellates reached dominance. In all cases *Ceratium* spp. reached the highest values of p_i; *Ceratium hirundinella* Schrank reached 0.98 in Pluβsee 1989 and 0.75 in Behler See 1990, *Ceratium furcoides* Langhans reached 0.90 in Pluβsee 1990. In contrast to Pluβsee, there were also some minor summer peaks of diatoms in Behler See. The greater importance of diatoms in Behler See can both been explained by higher Si:P or Si:N ratios (Sommer, 1983, 1985, 1989) or by longer mixing in spring and intermittent mixing events during summer (Reynolds, 1980, 1984, 1988).

If the biomass/capacity ratio is used as an operational, inverse measure of disturbance then not only wind induced mixing events but also internally driven reductions of biomass, such as the clear-water phase, qualify as disturbance. Figure 4 shows more or less reciprocal temporal changes of B/K and the diversity in both lakes. For the purpose of a cross-correlation analysis,
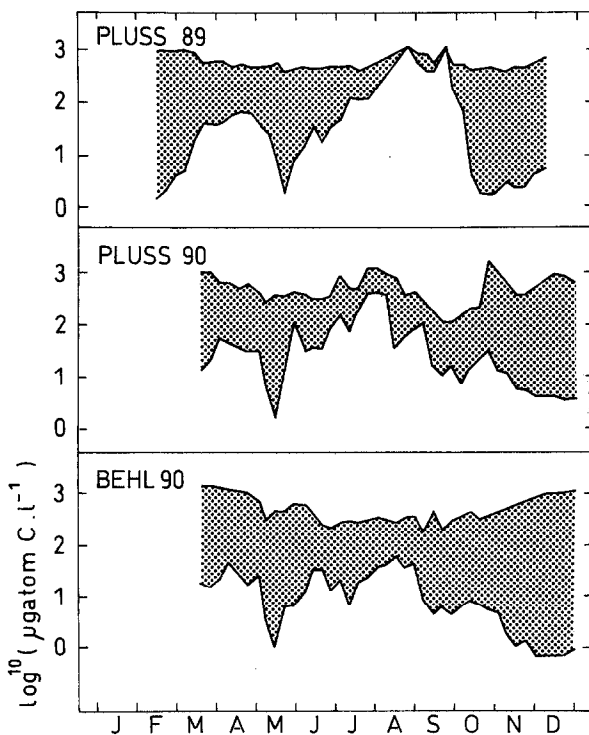

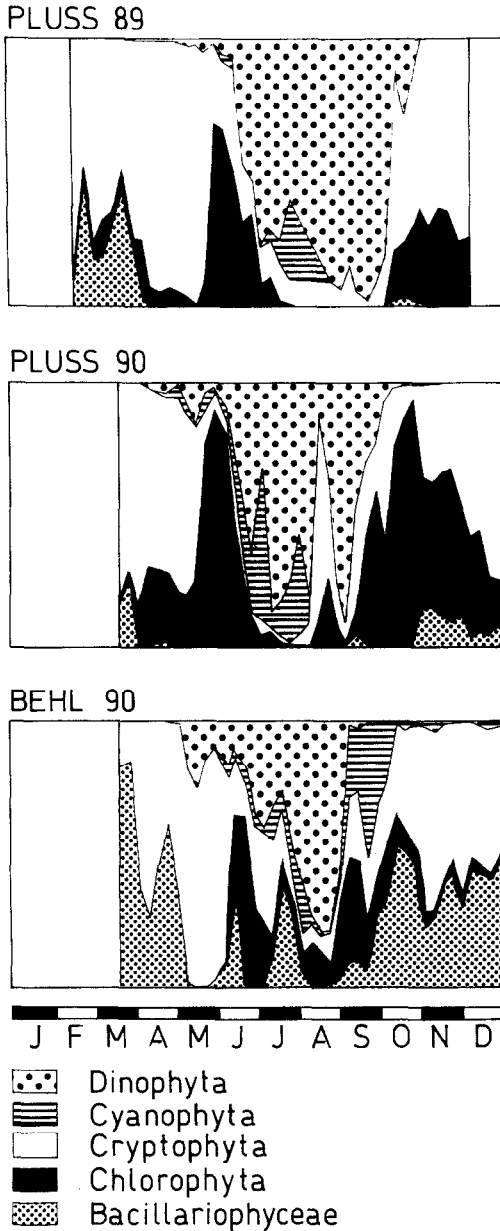*Fig. 2.* Phytoplankton biomass (in μgatom C calculated according to Rocha & Duncan 1985; lower limit of stippled area) and carrying capacity (calculated as $27 \cdot N_{to}$; upper limit of stippled area) in Behler See and Pluβsee; logarithmic scale.

PLUSS 89

PLUSS 90

BEHL 90

J F M A M J J A S O N D

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[···] Dinophyta
[≡≡≡] Cyanophyta
[   ] Cryptophyta
[███] Chlorophyta
[▒▒▒] Bacillariophyceae
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Fig. 3. Taxonomic composition of phytoplankton biomass in Pluβsee and Behler See.

Fig. 4. Diversity (H') and the biomass/capacity quotient (logarithmic scale) in Pluβsee and Behler See.

the time-series of $log_{10}(B/K)$ and H' were differenced; i.e. the original values were replaced by the difference between two successive values (Chatfield, 1984). Diff $log_{10}(B/K)$ and diff H' were then used as input variables in a cross-correlation analysis. This analysis showed significant negative correlations for all three lake-years with no time-lag. A regression analysis between diff
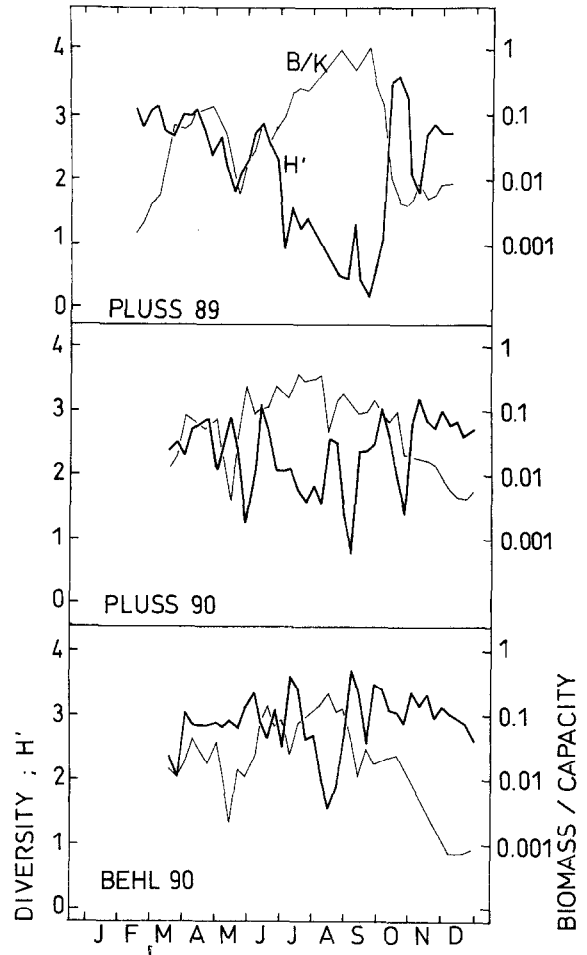
$log_{10}(B/K)$ and diff H' showed very similar (strongly overlapping standard errors) slopes and y-axis intercepts (Table 1). This indicates that the response of phytoplankton diversity to disturbances is similar in both lakes (Fig. 5).

The similarity in the diversity-disturbance relationship between both lakes also becomes evident from a scatter-plot of H' against log (B/C) (Fig. 5). When the biomass of phytoplankton reaches the carrying capacity diversity tends to become very low, the minimal recorded value being 0.16. Diversity begins already to decline when the biomass exceeds about 5%. If we accept the rationale of Hutchinson's (1961) paradox and of Connell's (1978) intermediate disturbance hypothesis, this means a surprisingly early onset

Table 1. Regression analysis of the week-to-week difference in diversity (y) on the weekt-to-week difference in $\log_{10}/BK$ (x) according to the model $y = a + bx$.

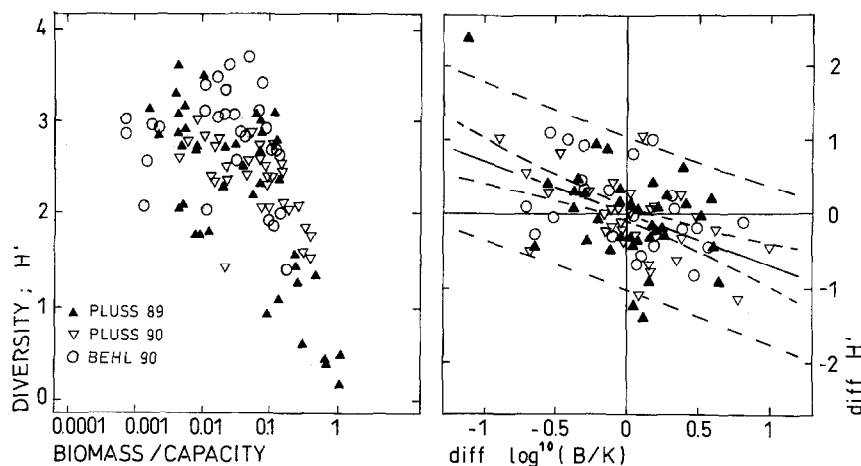| Lake/year	$a + SE$	$b \pm SE$	r	p
Pluβsee 1989	0.006 ± 0.091	-0.87 ± 0.26	-0.48	<0.002
Pluβsee 1990	-0.055 ± 0.084	-0.67 ± 0.20	-0.52	<0.005
Behler S. 1990	0.086 ± 0.107	-0.59 ± 0.26	-0.43	<0.05
All data	0.007 ± 0.053	-0.72 ± 0.14	-0.48	<0.00001

Fig. 5. Left: Diversity and B/K (logarithmic scale) in Pluβsee and Behler See. Right: Regression analysis of the week-to-week difference in H' on the week-to-week difference in $\log (B/K)$; the regression line and the 95% confidence intervals for the regression line and for the dependent variable refer to the entire data set (see Table 1).

of competitive exclusion while it takes 4 or 5 more doublings until competitive exclusion approaches completion. At B/C quotients <0.05 diversity fluctuates within relatively wide margins ($H' = 1.5$ to 3.7). There is a slight indication of a decline in diversity at very low B/K. This decline would be in agreement with the IDH, but the data are far from being convincing. Thus only one half of the IDH is fully supported: Diversity tends to decline, the longer the regime remains undisturbed.

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