

The intermediate disturbance hypothesis—species diversity or functional diversity?

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Phytoplankton dynamics in a shallow eutrophic lake were investigated over a 3-year period with respect to environmental forces which drive species composition and diversity. Diversity was calculated on the basis of species as well as on the basis of their functional properties (the C-R-S concept). Stratification and water column mixing had a strong impact on phytoplankton composition. Application of a similarity–diversity model revealed that a high diversity was a transient non-stable state, whereas drastic changes or long-lasting stable environmental conditions are characterized by low diversity. This effect was more pronounced when the diversity was calculated on the basis of the phytoplankton species' functional properties. Thus, this functional approach supports the intermediate disturbance hypothesis from field data.

INTRODUCTION

During the last decade many attempts have been made to explain phytoplankton dynamics and species diversity in lakes within the theoretical framework of the intermediate disturbance hypothesis [IDH (Padisák *et al.*, 1993)]. The IDH states that species diversity is low after a disturbance, when only a few species have survived or few colonizing species dominate under the new environmental conditions, or when the system has approached an equilibrium stage which is dominated by few species with high competitive abilities. Diversity is high when disturbances occur at an intermediate frequency or with intermediate intensity (Grime, 1973; Connell, 1978). In this respect, a drastic change in water column mixing depth can be regarded as a disturbance since it alters the competitive conditions through changes in nutrient and light availability (Reynolds, 1993). Experimental studies from the laboratory (Sommer, 1995; Polishshuk, 1999) and enclosure experiments (Flöder and Sommer, 1999) support the IDH, but the application of the IDH to field data implies some difficulties due to operational problems. In many cases the exact time of a disturbance cannot be determined, especially when samples are taken within fixed routine sampling intervals. Furthermore, it is difficult to

estimate the intensity of a disturbance. Thus, parameters are required which are independent from the disturbance itself, but which are indicators of the stage in phytoplankton succession. One approach is the ratio of phytoplankton biomass to the carrying capacity calculated from nutrient concentrations. A low ratio indicates an early stage in succession, whereas a high ratio is achieved in a final equilibrium stage of succession (Sommer, 1993). Another approach is the diversity–similarity relationship (Lindenschmidt and Chorus, 1998). This relationship is characterized as follows. A low similarity between temporally consecutive samples is the result of a drastic change in species composition, e.g. due to a disturbance. High similarity indicates stable or equilibrium conditions. Both, low and high similarity should be characterized by low diversity. When the species diversity is high, the similarity is supposed to be in an intermediate range, because changes in species composition are mainly due to competitive exclusion. Here we focus on a modified approach using the similarity and diversity relationship combined with an ecological or functional categorization of phytoplankton species. Functional diversity [*sensu* (Martinez, 1996)] is based on ecological, morphological and physiological properties of the algal cells instead of their taxonomic features. In terrestrial ecosystems, such as prairie

grasslands, it was shown that for several processes on the ecosystem level the functional diversity was of great importance (Tilman *et al.*, 1997).

METHOD

Study site

This study was conducted in the lake Flakensee near Berlin, Germany from 1994 to 1996. The lake is a eutrophic, hard-water lake with an area of 75.5 ha, a maximum depth of 8.5 m, a mean depth of ca. 4 m and a theoretical water residence time of 26 days. In early/mid-June a clear water phase regularly developed, with Secchi depth of >5 m. During the summer, pH did not exceed 8.5 due to the lake's hard-water status. Flakensee is a 'medium shallow' lake according to the classification of Nixdorf and Deneke (Nixdorf and Deneke, 1997) with periods of stratification during the summer depending on meteorological conditions. During stratification, soluble reactive phosphorus (SRP) and ammonium accumulated in the hypolimnion. Mean annual epilimnetic nutrient concentrations were 163 µg l⁻¹ total phosphorus (TP) and 815 µg l⁻¹ total nitrogen (TN) (Weithoff, 1998). During the summer the phytoplankton in Flakensee is moderately nitrogen limited, whereas phosphorus is almost always in high supply (Weithoff and Walz, 1999).

Light measurement, euphotic depth and mixing depth

Depth profiles of the underwater light intensity were measured with a Li Cor SA 193 spherical light sensor. The euphotic depth was calculated as the depth with 1% of surface irradiance. The thermocline was determined by measurements of temperature depth-profiles (Hydrolab H20), at $\Delta T \text{ m}^{-1} > 1^\circ\text{C}$.

Sampling, analyses and enumeration

From mid-May until mid-September of each of the years, weekly samples were taken from the epilimnion (above the thermocline) at vertical intervals of 1 or 0.5 m. For nutrient analyses, a subsample was filtered through a 0.45 µm membrane filter. SRP was analysed using the molybdate method, ammonium was analysed using the phenol-hypochlorite method, and nitrate was measured using ion chromatography (Zwirnmann *et al.*, 1999). Dissolved inorganic nitrogen (DIN) was calculated as the sum of nitrate and ammonium. Phytoplankton samples were fixed with Lugol's iodine and species composition and bio-volume were analysed with an inverted microscope offering 100 × to 1000 × magnification. Cell volume was calculated from cell measurements (up to 30 cells) by

applying simple geometric equations after Rott (Rott, 1981), except for *Ceratium hirundinella* and *Ceratium furcoides*. For these species a constant cell volume of 45 000 (Reynolds and Bellinger, 1992) and 41 000 µm³ respectively was assumed. In 1994, phytoplankton nanoplanktonic cells which were not determined to species or genus were counted in two size groups of 0–5 µm and 5–10 µm length. These were treated as two species when calculating the species diversity. Also in 1994, *Cryptomonas* spp. were counted in size groups. As the different *Cryptomonas* species differ in size, the biomass in each size group was assigned to species on the basis of the species determination and size measurements from 1995 and 1996. Phytoplankton diversity was calculated using the Shannon–Weaver Index (\log_2) H' on the basis of biomass (Sommer *et al.*, 1993). This was done separately for species and ecological strategists:

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

where p_i is the relative amount of biomass of each species i or each ecological strategy i . The classification of the functional properties was based on the C-, R- and S-concept according to Reynolds (Reynolds, 1988b, 1997) accounting for cell- or colony-size, susceptibility to zooplankton grazing, sedimentation rate, phosphorus uptake and maximal potential growth rates. The assignments of the species were according to Reynolds (Reynolds, 1997).

C-strategists are characterized by small cell size, high susceptibility to zooplankton grazing, high potential growth rates and low sedimentation losses. In Flakensee, abundant species of this group were *Cryptomonas* cf. *ovata*, *Cryptomonas marssonii* and *Rhodomonas minuta*. These cryptophytes exhibited high growth rates in an enclosure study performed in Flakensee in 1996 (Weithoff *et al.*, 2000).

R-strategists are characterized by large cell or colony size, low susceptibility to zooplankton grazing, high potential growth rates, and high sedimentation losses. Abundant species of this group were *Fragilaria crotonensis*, *Aulacoseira granulata* and *Asterionella formosa*.

S-strategists are characterized by large cell or colony size, low susceptibility to zooplankton grazing, low potential growth-rates and low sedimentation losses. Abundant species of this group were *Anabaena* spp. and *Ceratium* spp.

Thus, a high functional diversity indicates the co-occurrence of species with widely differing ecological features.

The similarity was calculated as the Renkonen number, RN (Müller, 1984):

$$RN = \sum \min(p_{it}, p_{it-1})$$

where p_{it} is the relative amount of species i or ecological strategy i at time t and p_{it-1} is the corresponding value at time $t-1$. Using relative abundances, only compositional changes are represented rather than changes in total

phytoplankton biomass. For the graphical presentation and statistics of the relationship between diversity (y values) and similarity (x values) the data pairs were grouped into five equally sized groups (20% percentiles) with ascending similarity, i.e. 20% (20–40%, 40–60% . . .); the similarity values of each percentile were combined and the respective mean of similarity and diversity values were calculated. The diversity and similarity indices were derived from the same measurements, i.e. the relative species composition which may give rise to mathematical interrelationships between the two indices potentially yielding spurious correlations. For the C-R-S case, we tested for systematic interdependencies between similarity and diversity using two different approaches. In the first approach, we generated numerically a time-series of 262 144 (2^{18}) random samples reflecting phytoplankton assemblages consisting of three categories. The relative contribution of each category representing one ecological strategy varied randomly between 0 and 1. From this time-series the similarity between all consecutive samples (t and $t-1$) was calculated and the diversity at t was plotted against the similarity. As for the field data, the data pairs were grouped in equally sized groups. For the second approach, we generated all possible combinations of the

relative contribution of each of the three categories in 0.05 increments, e.g. the relative contribution of C, R and S in sample 1 was: 1.0, 0.0, 0.0, in sample 2: 0.0, 1.0, 0.0, in sample 3: 0.0, 0.0, 1.0, in sample 4: 0.95, 0.05, 0.0; etc. ($n = 231$). Then, we paired each combination with all others, yielding in total 53 362 pairs from which the similarity and the diversity were calculated and plotted as in the first approach. This first approach revealed the stochastic relationship between similarity and diversity, whereas the second shows all possible combinations. We assume that potential deviations between the observed and the simulated relationships of diversity versus similarity are attributable to ecological mechanisms.

RESULTS

Water column stability

The meteorological conditions varied strongly between the years of investigation and they had a considerable impact on the water column stability. In 1994, high global irradiance led to an intense warming of the upper water layers resulting in a period of stable stratification from July until mid-August (Figure 1). The differences in water

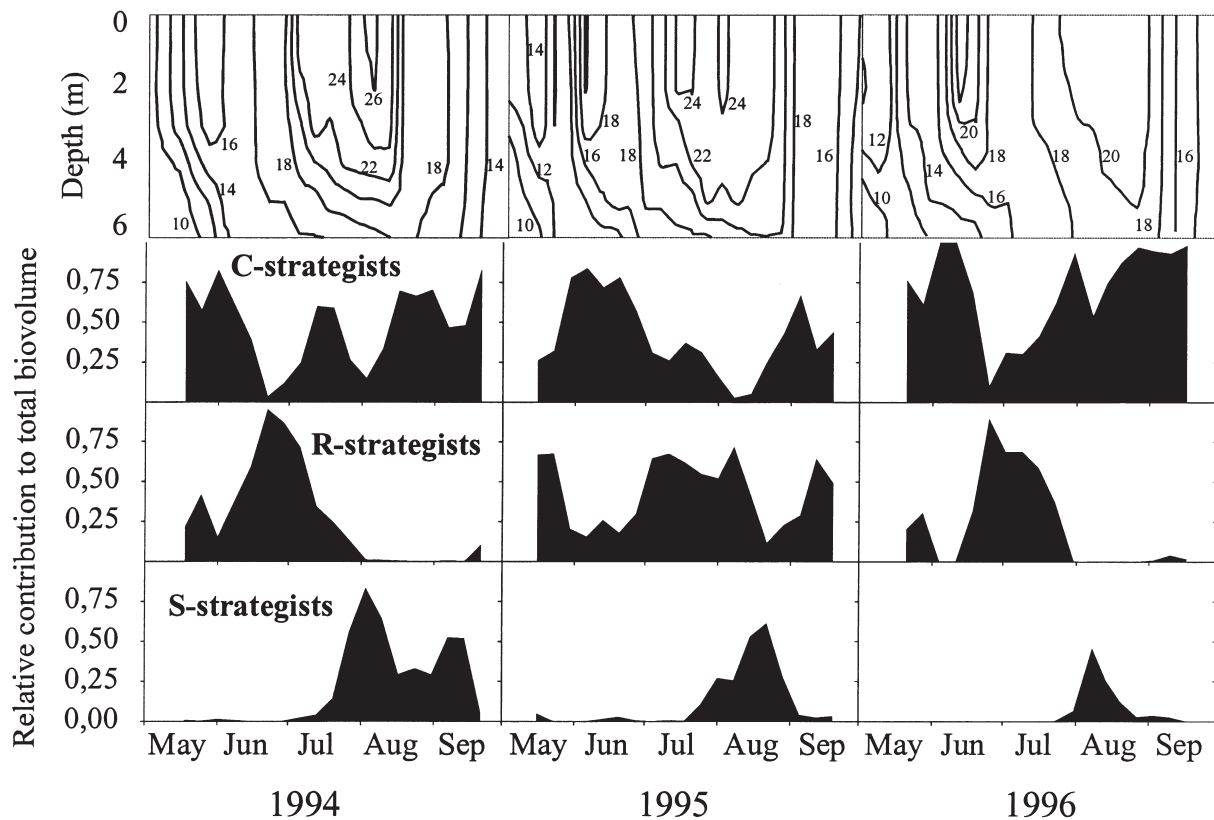


Fig. 1. Temperature isopleths (°C; top) and seasonal dynamics of phytoplankton ecological strategies (bottom) from May to September in 1994–1996.

temperature between surface and lake bottom (6 m) were about 10°C with surface temperatures up to 26°C. During this period the hypolimnion became anoxic and dissolved nutrients accumulated in the deeper water layers. In 1995, global irradiance was less intense and wind velocity was higher than in the previous year. Consequently, stratification was less stable, mixing depth was often higher than in 1994 and the temperature difference between surface and lake bottom was $\leq 7^\circ\text{C}$. The summer of 1996 was characterized by low temperatures and sporadic strong winds. No stable stratification developed, only periods of slight stratification occurred with low vertical temperature differences due to lower surface temperatures. A strong wind event in early July 1996 caused a complete water column mixing with a subsequent weak restratification. In all years 'autumn' holomixis took place in mid- to late August.

Phytoplankton succession

The phytoplankton assemblage subdivided among the ecological strategies was similar in all years from May until mid-June but differed strongly in July and August between years (Figure 1). Before and during the clear-water phase (early June), C-strategists dominated the phytoplankton community. These were mainly *Cryptomonas* cf. *ovata* and *C. marssonii*. In late June R-strategists such as *Fragilaria crotonensis* and *Asterionella formosa* (only 1996) were dominant in all three years. In 1994—the year with several weeks of stable stratification—the R-strategists were replaced by a short period of C-strategists dominance before S-strategists became dominant. These were mainly

Ceratium hirundinella and *Anabaena* spp. They declined when autumn mixing began. The phytoplankton assemblage in July/August 1995 differed from 1994. The dominance of R-strategists lasted until August but *F. crotonensis* was replaced by *Aulacoseira granulata* followed by a peak of S-strategists made up of *C. hirundinella*. Almost no cyanobacteria occurred. After water column mixing in late August 1995, first a peak of C-strategists and then of R-strategists were observed. In 1996—the year with weak stratification and intermittent holomixis—C-strategists dominated from mid-July until September. S-strategists were subdominant in August and R-strategists were almost absent after their decline in July.

Nutrients

DIN concentrations in the epilimnion were low throughout all summers and showed only slight variation between years (Figure 2). DIN declined during the spring algal development to levels below the detection limit of the method and increased during the clear-water phase in early June. The maximum DIN concentration during the clear-water phase was relatively constant between years and ranged from 220 to 263 $\mu\text{g l}^{-1}$. After the peak in June, DIN concentrations fell again to low levels and remained low until the input of ammonium-rich hypolimnetic water due to August water column mixing. Since in 1996 ammonium accumulated to a much lesser extent in the hypolimnion than in the previous years (Weithoff, 1998), August mixing did not lead to an increase in epilimnetic DIN concentrations. In contrast to DIN, the concentrations of SRP were high for long periods throughout the

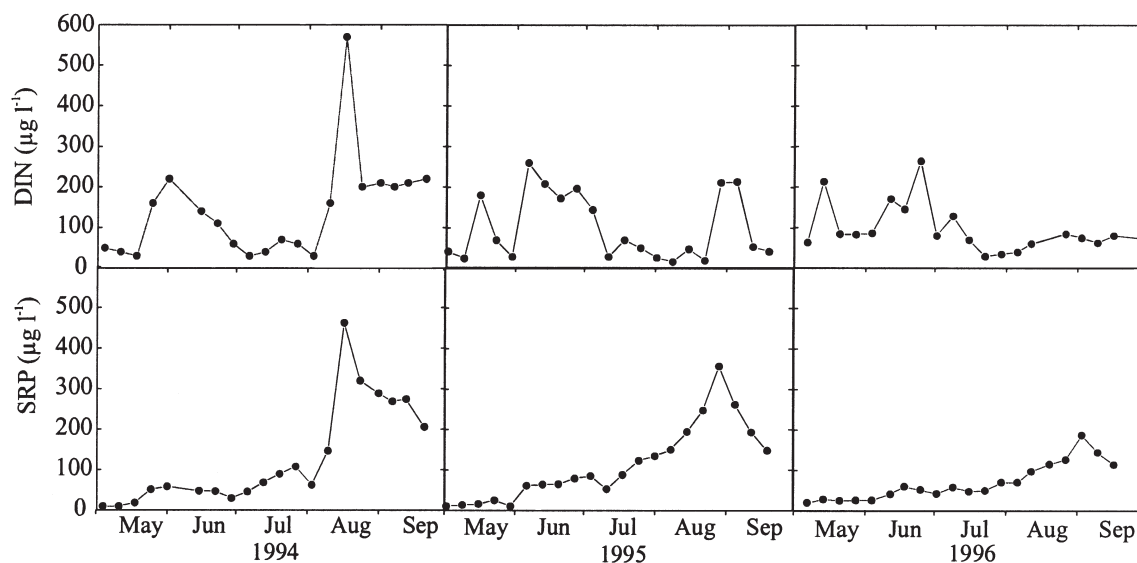


Fig. 2. Time course of epilimnetic dissolved inorganic nitrogen (DIN, top) and soluble reactive phosphorus (SRP, bottom) concentrations from May to September 1994–1996.

three summers. SRP concentrations rose also during the clear-water phase but remained high ($>50 \mu\text{g l}^{-1}$) until August mixing when—similar to DIN—the input of nutrient-rich hypolimnetic water led to a further increase in SRP levels (Figure 2). As for DIN, the SRP concentrations during the clear-water phases were relatively constant between years and ranged from 58 to $65 \mu\text{g l}^{-1}$.

Light availability

The highest ratios of euphotic depth to mixed depth ($Z_{\text{eu}} : Z_{\text{mix}}$) were found in June in each year due to high water transparency (Figure 3). Low $Z_{\text{eu}} : Z_{\text{mix}}$ ratios (indicating light limitation of phytoplankton growth) were observed when mixing depth was high, mainly in late August and September, as well as during holomixis in July 1996. During the other periods the $Z_{\text{eu}} : Z_{\text{mix}}$ ranged from

1 to 4, suggesting no light limitation. Thus, the light availability was also strongly dependent on water column mixing.

Phytoplankton diversity, similarity and mixing depth

Phytoplankton diversity varied from May to September, both calculated on the basis of species and on the basis of ecological strategies (Figure 4). On a species basis, diversity tended to be high in periods of high mixing depth and low when the mixing depth was low. This pattern was, however, not consistent throughout the whole investigation period. In 1995, species diversity was high when August mixing started but declined during August mixing in 1996. Also, the diversity on the basis of ecological strategies showed no close relationship to mixing depth

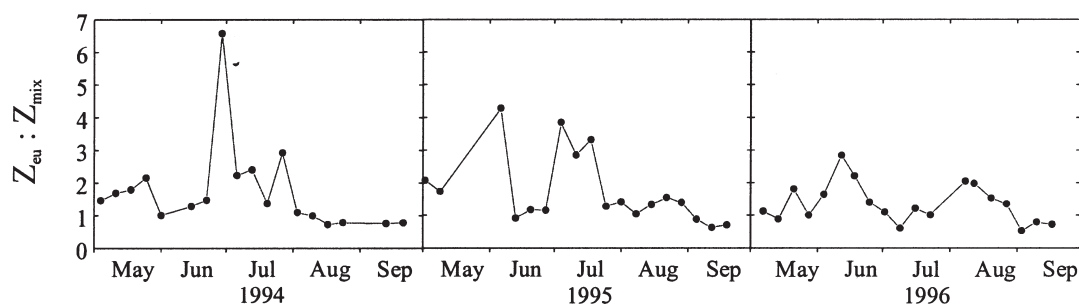


Fig. 3. Time course of the ratio of euphotic depth to mixing depth ($Z_{\text{eu}} : Z_{\text{mix}}$) from May to September 1994–1996.

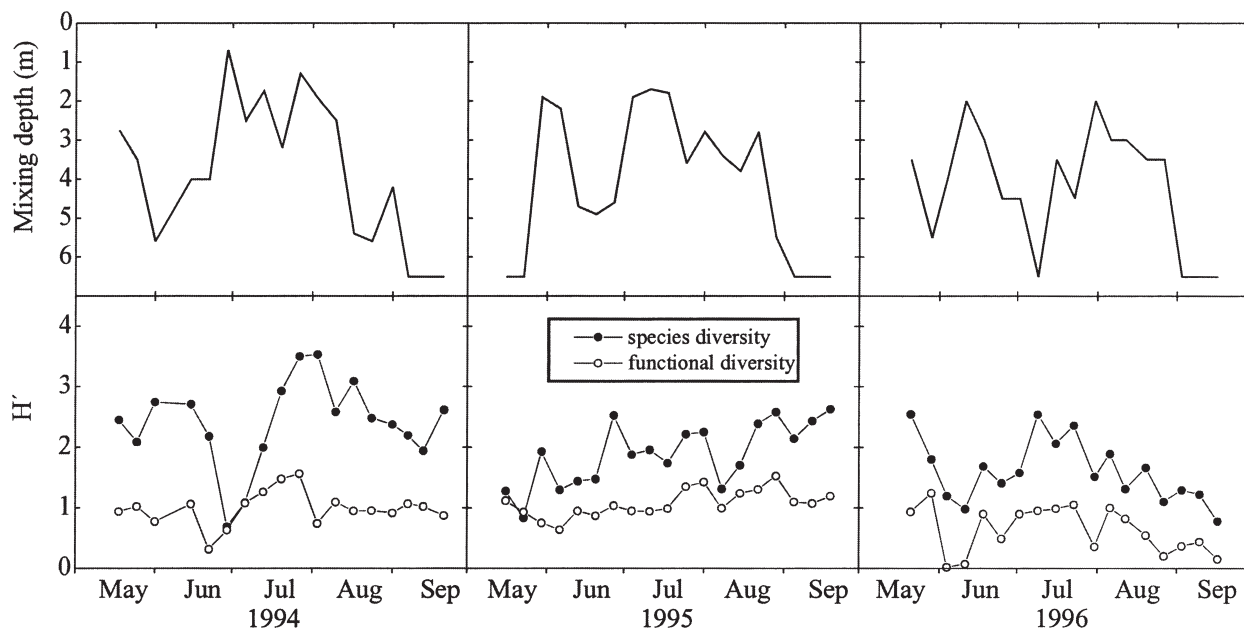


Fig. 4. Time course of mixing depth and species diversity and functional diversity from May to September 1994–1996.

(not significant, Spearman rank correlation). Thus, mixing depth alone was not sufficient to explain phytoplankton diversity.

The diversity–similarity relationship from random samples (approach 1 in method section) exhibited a wide scatter with an increasing diversity with increasing similarity up to a similarity of about 0.8. At higher similarities diversity remained constantly high (mean >1.4, Figure 5a). A similar outcome was observed when all possible combinations in 0.05 steps were generated (approach 2). The maximum diversity was found at a similarity of 0.7 and remained high (mean >1.2) with increasing similarity. A diversity close to the maximum possible value is mathematically impossible at a very low similarity (upper left area in Figure 5 a, b). This derives from the fact that extremely low values of the similarity arise only when the

relative species contribution changes from a pronounced dominance of one category to another. Under such conditions the diversity is always well below its maximum. Neither of these two approaches exhibited a decline in diversity at high similarity.

The relationship between species diversity and similarity calculated from Flakensee phytoplankton data exhibited a curved pattern (Figure 6a). A low diversity was found when the similarity was high, and a high diversity was observed in an intermediate range of similarity. A combination of low diversity and low similarity did not occur. This indicates that high diversity was a transient non-stable state. This pattern was more pronounced when the functional diversity rather than species diversity was plotted against the similarity (Figure 6b). Though there was also a wide variation, a distinct bell-shape pattern was

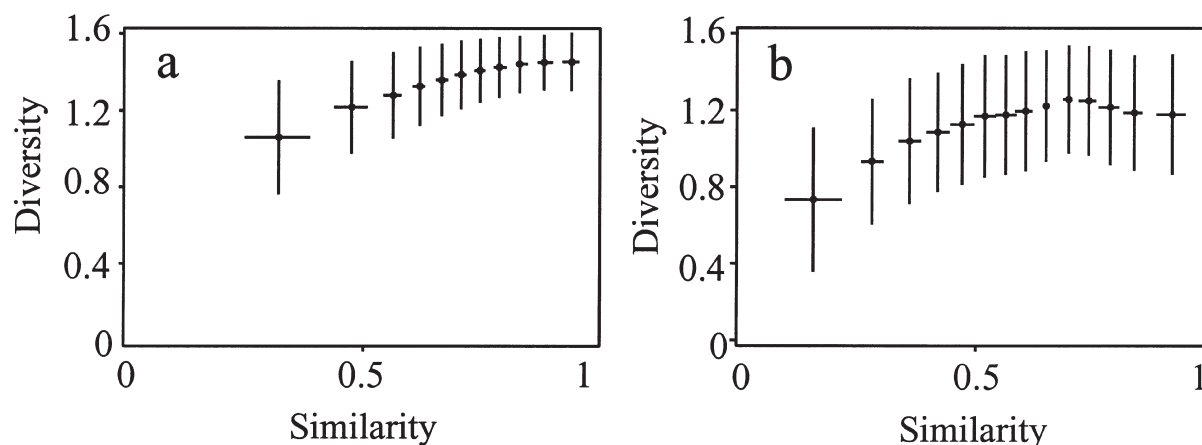


Fig. 5. Relationship between the diversity and similarity from numerically simulated samples consisting of three categories. Mean \pm SD of equally sized groups, see Method section. (a) Results from 262 144 random samples, (b) results from all possible combinations of three categories with 0.05 increments of relative abundance ($n = 53\,362$).

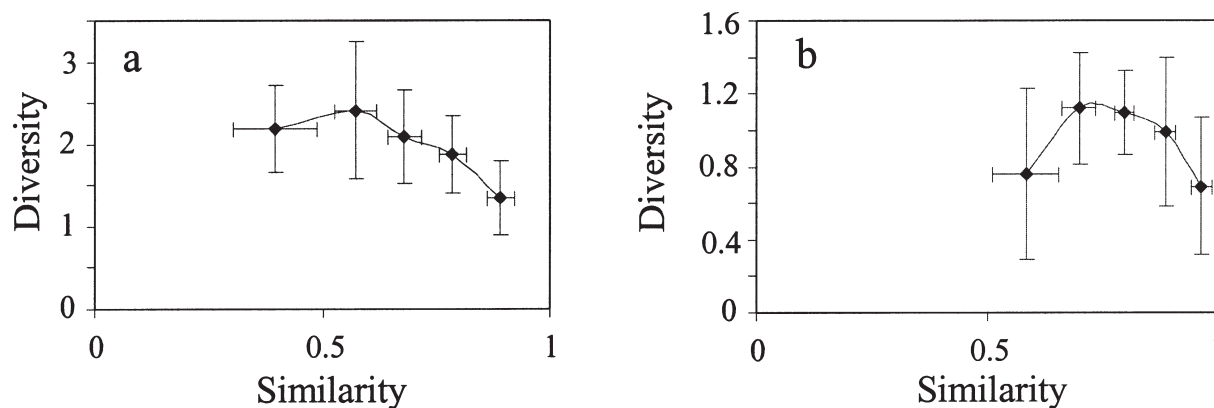


Fig. 6. Relationship of lake phytoplankton diversity and similarity on the basis of species (a) and on the basis of ecological strategists (b). Data were pooled for all sampling dates from May to September 1994–1996 and calculated as 20% percentiles along the similarity axis, see Method section. Error bars \pm SD.

found. With increasing similarity from 0.8 to 1 a strong decline in functional diversity appeared (mean <0.7). In both cases, species and strategies, the diversity between the 20% similarity percentiles was significantly different ($P < 0.05$, Kruskal–Wallis test).

DISCUSSION

Variability in meteorological conditions led to interannual variations in water column stability and stratification pattern in Flakensee. Long periods of stratification (>2 months) caused high accumulation of nutrients in the hypolimnion (Weithoff, 1998) and the availability of these nutrients in the upper water layers was dependent on the mixing of the water column. As inorganic nitrogen was in short supply—except during the clear-water phase—and phytoplankton was often nitrogen limited (Weithoff and Walz, 1999) intermitted mixing events can be regarded as nutrient pulses supporting phytoplankton growth.

Combining the results from water column stability (stratification pattern) and phytoplankton succession on the basis of their ecological strategies the following pattern appears. The more stable the stratification the greater the relative success of S-strategists and the more unstable the stratification the higher the share of C-strategists. In 1994 when the water column was stratified for several weeks highly competitive species became dominant. During the following two summers no such stable conditions occurred and the phytoplankton succession did not reach the final stage. This is consistent with the theory of phytoplankton succession in lakes (Sommer *et al.*, 1986; Reynolds, 1988a, 1993).

The observed variability in stratification, together with a similar seasonal pattern in nutrient availability, facilitates the investigation of external disturbances on phytoplankton succession especially with respect to the intermediate disturbance hypothesis in the light of the phytoplankton diversity–similarity relationship.

No distinct relationship was found between mixing depth and diversity. In some cases, however, increased mixing depth and high diversity coincided. Either there was no such relation or a simple comparison of water column mixing on diversity is not sufficient to detect a possible influence of mixing on phytoplankton diversity. For example, if a disturbance causes a shift in species composition, the diversity before and after this disturbance might be the same. Thus, a dynamic variable is necessary, such as the similarity index which provides information about compositional changes between two consecutive sampling dates. Furthermore, species diversity at different times of the season can be similar, though the species composition differs strongly and represents different

stages of succession. At dominance of *Anabaena* spp. and *Ceratium*—both S-strategists prevailing in early August 1994—diversity might be similar to a situation in which *Cryptomonas* and *Fragilaria* (one C- and one R-strategist) dominate, but in the latter case the functional diversity will be higher. To overcome this phenomenon, the similarity–diversity relationship from Lindenschmidt and Chorus (Lindenschmidt and Chorus, 1998) was expanded by the inclusion of the functional diversity in the present study. A high functional diversity indicates the co-occurrence of species with widely differing ecological demands and reflects the ecological diversity in the sense of the IDH in a much better way. Using this approach the organization of plankton communities can be explained from field data within the framework of the intermediate disturbance hypothesis. The validity of this conclusion was tested by contrasting the pattern observed in the field data with those obtained from random numbers. It was proven that the decline in diversity at high similarity found in the lake data is not a consequence of mathematical interdependencies but of ecological mechanisms. It should be pointed out that a low diversity at high similarity does not necessarily indicate a late successional stage. In August/September 1996, when mixing depth was high, C-strategist (cryptophytes) dominated for several weeks and thus similarity was high and diversity was low. Cryptophytes often dominate phytoplankton after disturbances and they have the potential to occur persistently (Barbiero *et al.*, 1999).

The occurrence of particular functional groups could be largely explained by the mixing regime but other factors, such as zooplankton grazing, also affect phytoplankton biomass and species composition. Borics *et al.* (Borics *et al.*, 2000) found some evidence that changes through the trophic cascade after a fish-kill were responsible for an increase in phytoplankton functional diversity in a small hypertrophic pond. It is still a matter of debate whether zooplankton grazing should be considered as a disturbance or not. There is a lack of information concerning under which conditions herbivory leads to an increase or a decrease in phytoplankton diversity. However, size-selective grazing undoubtedly influences phytoplankton diversity as cell sizes differ between species. Weithoff *et al.* (Weithoff *et al.*, 2000) showed that zooplankton grazing in artificially mixed enclosures in Flakensee have dampened the mixing effect on phytoplankton diversity; when herbivory was low, mixing reduced phytoplankton diversity relative to undisturbed control enclosures whereas a high level of herbivory prevented fast growing species from a strong net increase in biomass and diversity did not differ from undisturbed enclosures. In another enclosure study it was shown that *Daphnia* abundance influenced phytoplankton diversity and species

richness (Flöder and Sommer, 1999). In an experimental study on benthic microalgae Sommer (Sommer, 1999) found that different feeding types of herbivores had a different impact on algal diversity. Model studies suggest that predators influence and maintain diversity of their prey (Caswell, 1978; Leibold, 1996).

The consequences of a high phytoplankton diversity for herbivores are weakly understood. A mixed diet of diatoms and flagellates reared at different Si : N ratios enabled high production of the rotifer *Brachionus plicatilis* when both groups accounted for an equal share of biomass, whereas dominance by one group as a result of competitive exclusion due to very high or very low Si : N ratios enabled low *B. plicatilis* production (Sommer, 1998). This was also found for the rotifer *B. calyciflorus* with a mixed diet of laboratory-grown algae, even when cyanobacteria, which were proved to be a poor food source when fed as a single food, were added to a suitable food source (Rothhaupt, 1991; Weithoff and Walz, 1995).

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