

Diversity in planktonic communities: An experimental test of the intermediate disturbance hypothesis

Sabine Flöder

Institut für Meereskunde, Abteilung Meeresbotanik, Düsternbroker Weg 20, D-24105 Kiel, Germany; and the Max-Planck Institut für Limnologie, August-Thienemannstraße 2, D-24306 Plön, Germany

Ulrich Sommer

Institut für Meereskunde, Abteilung Meeresbotanik, Düsternbroker Weg 20, D-24105 Kiel, Germany

Abstract

According to Connell's intermediate disturbance hypothesis (IDH), diversity within a community is maximal at intermediate frequencies and intensities of disturbances. In order to test the IDH, disturbances of different frequencies and intensities were imposed on natural plankton communities in controlled field experiments. These disturbances consisted of an artificial deepening of the mixed layer, leading to the dilution of epilimnetic populations and to a higher level of nutrients. Intervals between disturbances ranged from 2 to 12 d. Different intensities of disturbance were caused by differences in the experimental mixing depth (150 and 225% of the original epilimnion depth). Investigation focused on the effect that disturbances had on the diversity of natural phytoplankton communities. Additionally, we were interested in determining the effect of grazing by zooplankton. The results of the field experiments show for the first time the applicability of the IDH to phytoplankton within complete planktonic communities. Diversity showed a clear maximum at the intermediate disturbance interval of 6 d. Similarly, species number peaked at intermediate interval length (6–10 d).

The search for the causal explanation for species diversity and for its maintenance in natural systems is one of the key questions in modern ecology. There is a contrast between the obvious variety of species existing in natural systems and the competitive exclusion principle (Hardin 1960), which predicts that competition selects for the fittest species and leads to the exclusion of all the others. In aquatic ecology, this phenomenon is widely known as Hutchinson's paradox of the plankton (Hutchinson 1961). A wealth of community theories have been developed to address this paradox. Two types of approach dominate the theoretical development. The most widespread approach assumes the existence of stable equilibria in natural systems. Under the equilibrium assumption, the maintenance of diversity is explained by factors such as niche differentiation or natural enemies. These factors tend to reduce competition so that exclusion does not occur. On the other hand, approaches have been developed that remove the steady-state assumption and focus instead on transient dynamics and stochastic descriptions (Chesson and Case 1986). Hutchinson (1961) suggested that environmental changes could prevent phytoplankton diversity from reaching a state of stable equilibrium if those changes are frequent enough to reverse competitive hierarchies before exclusion occurs (Sommer et al. 1993).

According to the intermediate disturbance hypothesis

(IDH) (Paine and Vadas 1969; Connell 1978), a central non-equilibrium community theory, competitive exclusion reduces diversity in the absence of disturbance. Disturbances that are too intense or too frequent reduce species number and diversity, because only a few pioneer species are able to become established. Disturbance at intermediate frequency and intensity permits the coexistence of successful competitors and of competitively inferior pioneer species, because the former are not extinguished by the disturbances and the latter find repeated opportunities for recovery after disturbance. Therefore, intermediate disturbance should result in maximal diversity.

The IDH was originally developed for tropical rain forests and coral reefs. In these systems, the deaths of sessile organisms open new space that can subsequently be used for colonization by other organisms. Therefore, the spatial dimension of the resulting patch-dynamics is important for the diversity of the whole system. When focusing on the development of a single patch, the temporal dimension is of importance. Compared to sessile communities, patches in planktonic communities are more ephemeral because of turbulent mixing. Thus, temporal variability of environmental conditions seems more important for the maintenance of diversity than does spatial heterogeneity, especially in small lakes with uniform basins and no prominent horizontal environmental gradients.

Disturbance is a fundamental conceptual element of any nonequilibrium community theory, but the definition of disturbance is still controversial. Disturbance has been defined as the mechanism that causes mortality or partial destruction of biomass (Grime 1979; Kilar and McLachlan 1989), as a temporally discrete event that removes organisms and makes space or other resources available (Townsend and Hildrew 1994), or as a primarily abiotic, stochastic event that causes

¹ Present address: Center for Ecological Research, Kyoto University Kamitanakami Hirano-cho 509-3, Otsu, 520-2113, Japan.

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distinct and abrupt differences in species composition (Reynolds et al. 1993). The attempts to define disturbance are in disagreement regarding the mechanisms of disturbance, which may differ with respect to the community studied. However, there seems to be a consensus that disturbance is connected to environmental variability. In our context, we define disturbance as externally forced, episodic environmental variability. The classic example of disturbance, defined in this manner, is the increase of mixing depth caused by stormy weather or surface cooling (Reynolds 1984). Such mixing events cause the dilution of the epilimnetic populations and result in a pulselike increase in nutrient level and a change in the vertical mean light intensity in the epilimnion. In temperate regions of the northern hemisphere, the grand mean of the occurrence of spells of bad weather is 5–15 d (Harris 1986).

Experimental tests of the IDH have usually taken the form of laboratory experiments with one trophic level only (Robinson and Sandgren 1983; Gaedeke and Sommer 1986; Sommer 1995). Those studies confirmed the IDH for one-trophic level systems.

In order to investigate whether the IDH is applicable to phytoplankton communities in the presence of higher trophic levels, we performed two enclosure experiments with natural plankton communities. The experiments were carried out during the summer stratification period in Lake Plußsee (North Germany). The water column within the enclosures mimicked the natural stratification of the lake and contained the natural plankton community found in the season of the experiments. Experimental disturbances consisted of an artificial deepening of the mixed layer (Reynolds et al. 1984). This deepening was enforced at different frequencies and intensities.

Experimental design

Lake Plußsee (the study site) is an eutrophic headwater lake. It is situated in a valley and is sheltered by trees. Because of the effective wind shelter and the morphometric characteristics of the lake basin (funnel shaped; surface area, 14.3 ha; maximum depth, 29.2 m), Lake Plußsee usually shows a very stable summer stratification. The depth of the epilimnion is about 4 m (Krambeck et al. 1995).

The enclosures consisted of polyethylene tubes (Trikoron S, BP Chemicals) that were 1 m in diameter and had a length of 15 m (in experiment 1) or of 10 m (in experiment 2). Stabilized by metal rings, the enclosures were installed at a pontoon near the greatest depth of the lake. Pontoons were oriented in an east–west direction so that we could obtain a comparable light supply in each of the enclosures. The enclosures were open at the base in order to allow the exchange of nutrients with the surrounding hypolimnetic water. A net with 100- μm mesh on the bottom excluded larger predators of herbivorous zooplankton (such as *Chaoborus*, *Rutilus rutilus* and *Perca fluviatilis*) and retained the >100- μm fraction of zooplankton inside (Mumm and Sell 1995). The collapsed enclosures were lowered down to a depth that equaled the length of the enclosures (experiment 1) or to a depth just above the anoxic depth, i.e., H_2S present (experiment 2) and

were filled by slowly pulling the top ring through the water column (Grice et al. 1980). All enclosures were filled on the same day. Thus, the inoculum of the enclosures consisted of the natural planktonic community present at the starting time.

Disturbances were imposed by breaking the thermocline, using compressed air bubbles (1 bar liter⁻¹, 3 min), at different frequencies (2-, 4-, 6-, 8-, 10-, and 12-d intervals), while undisturbed enclosures served as controls. Different treatments were randomly arranged at the pontoons (Hurlbert 1984). Since there was more space at the pontoons than there were planned treatments, a few treatments could be replicated. The experimental mixing depth varied between experiments. In experiment 1 (from 20 July 1995–25 August 1995), the original mixing depth (4 m) was increased to 9 m, which corresponded to a 225% increase in the mixing depth. In experiment 2 (from 10 July 1996–15 August 1996), the original mixing depth (4 m) was increased to 6 m, which corresponded to a 150% increase in the mixing depth. The resulting disturbance intensity was measured as the relative increase of limiting nutrient concentrations caused by mixing. The duration of experiments was 36 d. The end of the experiment was not reached at the same day in each treatment because of the differing interval lengths. Each treatment finished at the end of an interval, resulting in the 10-d treatment ending on day 30 and the 8-d treatment ending on day 32.

Phytoplankton and nutrient samples were taken every second day and immediately after each disturbance as mixed samples from different depths (0.5 m, 1.5 m, and 3.0 m) in the epilimnion. Zooplankton was caught with a 100- μm mesh net every 12 d. Because of the shortness of the experimental treatment (3 min) and the quick restoration of the epilimnion temperature (<4 h), the depth of the mixed zone was considered to be 4 m before and after the disturbance as well. Light profiles were measured as $\mu\text{E m}^{-2} \text{ s}^{-1}$ photosynthetically active radiation (PAR) using a LI-193 Sa lightmeter. Light intensity was measured at five depths (0, 1, 2, 3, and 4 m), and the arithmetic mean was calculated for the mixing depth. Thus, the change in the light intensity of the mixed layer is based on the dilution of epilimnetic phytoplankton communities. Changes in the mixing depth itself did not contribute to the changes in light intensity.

Nutrient analyses were made using a Technicon continuous-flow system (Albrecht and Overbeck 1969). Total dissolved components were used as a measure of the nutrient availability in spite of the preference for inorganic sources of many phytoplankton species, because some species may also use organic nutrient sources (Berman 1988; Antia et al. 1991). Zooplankton was counted following the method outlined by Bottrell et al. (1976), and phytoplankton was counted according to the method of Lund et al. (1958). We concluded the counting of phytoplankton after we reached the 400th individual. Phytoplankton species were counted at three different magnifications (large species: $\times 160$; medium-sized species: $\times 250$; small species: $\times 400$). Since counting of phytoplankton at different magnifications means analyzing different volumes of the sample, the measure of species number had to be standardized. Each species with an abundance that equaled or exceeded the finding of a single in-

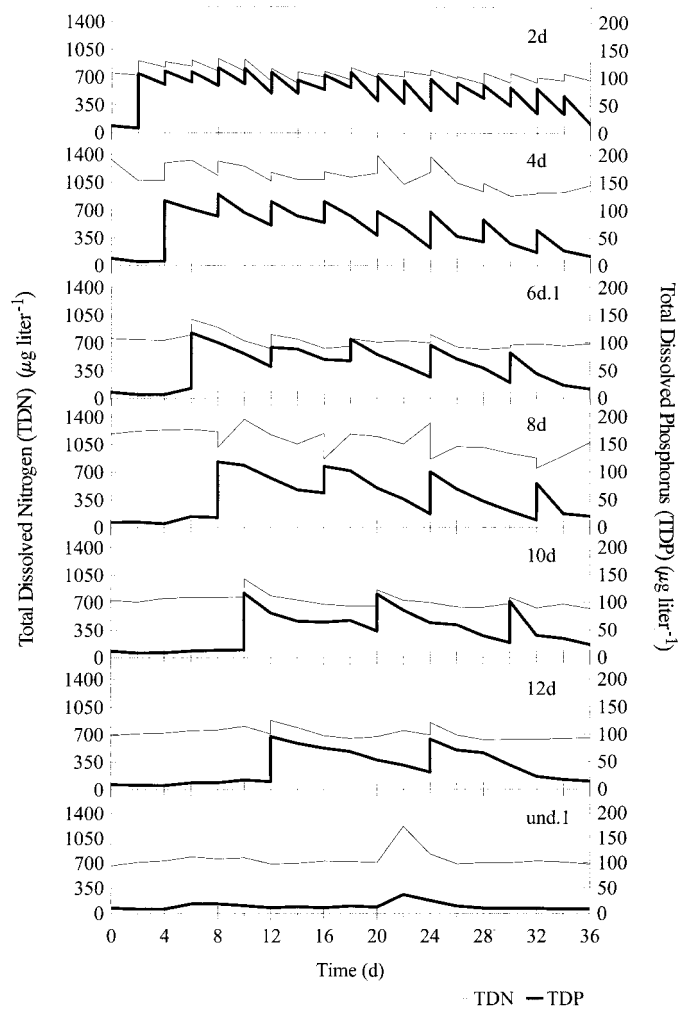


Fig. 1. Time course of nutrient concentrations during experiment 1. Thin line: total dissolved nitrogen (TDN); thick line: total dissolved phosphorus (TDP). 2–12 d: length of the disturbance interval in days; und.: undisturbed blank; ×.1: No. of the replicate. For better visualization, only one replicate of the day 6 and day 12 disturbance interval and of the undisturbed treatment is shown.

dividual at the highest magnification was considered to be present. Phytoplankton counts were converted into relative abundances on the basis of organism density. The index of diversity was calculated according to the method of Shannon and Weaver ($H' = -\sum p_i \ln p_i$; where H' signifies the Shannon index of diversity; p_i signifies the relative abundance of species i ; and $p_i = N_i/N_{tot}$) (Washington 1984).

The significance of the response of diversity and species number was tested by multiple regression analysis with a stepwise variable selection (backward procedure, F to remove = 4). Independent variables were entered in linear and squared form in order to account for the humped response predicted by the IDH.

Results of field experiments

Experimental disturbances result in pulselike increases in nutrient concentrations (Fig. 1) and changes in the vertical

Table 1. Disturbance intensity. Time averaged increase of total dissolved phosphorus (TDP) content (in %) caused by the experimental deepening of the epilimnion. Experiment 1, 225% increase of the natural mixing depth (4 m); Experiment 2, 150% increase of the natural mixing depth.

Disturbance interval (d)	Replicate number	Mean increase of TDP content (%)	
		Experiment 1 (225% increase of mixing depth)	Experiment 2 (150% increase of mixing depth)
2	1	128	14
4	1	257	95
4	2		50
6	1	204	105
6	2	269	129
8	1	364	142
8	2		182
10	1	384	182
12	1	390	151
12	2		291
und.*	1	0	0
und.*	2	0	0

* und., undisturbed blank.

mean light intensity in the epilimnion. Total dissolved nitrogen:total dissolved phosphorus (TDN:TDP) ratios clearly exceeded 7:1 in weight, indicating that phosphorus rather than nitrogen would be limiting (Redfield 1958). The two levels of experimental mixing depth (225% [experiment 1] and 150% [experiment 2] increases in the natural mixing depth) in combination with the different frequencies of disturbance (2–12-d intervals) resulted in gradients of disturbance intensity, measured as the increase of the limiting nutrient concentration (Table 1). The time-averaged size of TDP pulses corresponded to a 128–390% increase in the individual bags in experiment 1 and in a 14–291% increase in the individual bags in experiment 2. Thus, both experiments combined provided a continuous gradient of disturbance intensities from 14 to 390%. The biggest change in light intensity as a result of the experimental disturbance occurred in the treatments that were disturbed every second day (experiment 1: 7.5% relative change; experiment 2: 11.3% relative change). Treatments with a lower frequency of disturbance showed smaller changes in light intensity (experiment 1: 2.4–6.4%; experiment 2: 3.3–8.3%). In all cases, the relative light change was much weaker than was the nutrient change.

Zooplankton abundances (Fig. 2) appeared to be low in both experiments (*Daphnia*—experiment 1, $\bar{x} = 2.1 \times 10^4 \text{ m}^{-2}$; experiment 2, $\bar{x} = 6.3 \times 10^4 \text{ m}^{-2}$; calanoid copepods—experiment 1, $\bar{x} = 4.8 \times 10^4 \text{ m}^{-2}$; experiment 2, $\bar{x} = 4.6 \times 10^4 \text{ m}^{-2}$), although there was an increase in *Daphnia* abundance during the first 24 d of experiment 2. In this experiment, *Daphnia* abundance peaked at day 24 ($14.3 \times 10^4 \text{ m}^{-2}$) and then declined until day 36 ($1.2 \times 10^4 \text{ m}^{-2}$). No systematic trend related to the disturbances was detected in zooplankton abundance. However, between enclosures, differences appeared to be considerable (Fig. 2).

Phytoplankton abundance followed a similar pattern in

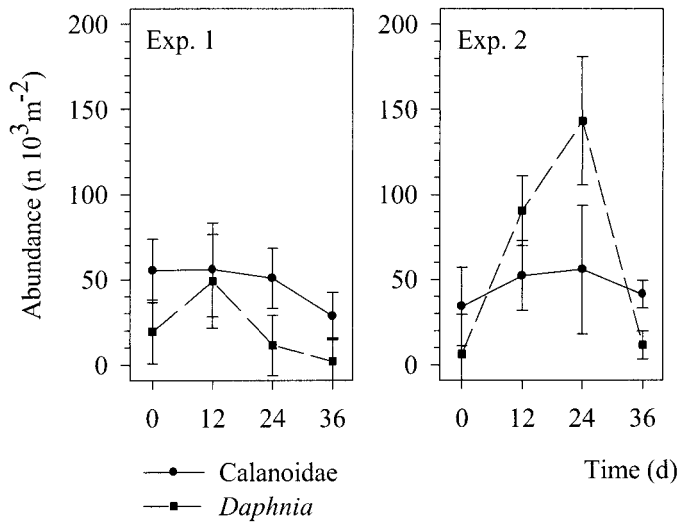


Fig. 2. Abundances of the most important herbivorous zooplankton in the course of the experiments. Data were averaged over all treatments and controls, since there was no systematic trend related to the mixing events. Bars represent the standard deviation. Experiment 1: 225% increase of the natural mixing depth (4 m); experiment 2: 150% increase of the natural mixing depth.

both experiments (shown for experiment 1, Fig. 3). In the beginning, the phytoplankton consisted mainly of *Cyanodictyon imperfectum*, *Oocystis parva*, and *Chrysochromulina parva*. During the course of the experiment, *Cyanodictyon* became dominant in the enclosure that was disturbed every second day and became highly abundant in the nonmanipulated enclosures. Algal abundances were more balanced in the enclosures with a 6-d interval, and *Anabaena spiroides* was detected, in addition to the initially common species. With regard to the dominant species (*C. imperfectum* and *O. parva*), the species structure appeared to be fairly robust to the disturbance. The abundance of these species and minor phytoplankton species were affected by disturbance. The observed levels of phytoplankton diversity and species number at the end of the experiments (Fig. 4) were in accordance with the prediction of the IDH. In both experiments, the H' showed a clear maximum at the intermediate disturbance interval of 6 d (experiment 1: $H'_{rep2} = 2.49$ and $H'_{rep1} = 2.56$; experiment 2: $H'_{rep2} = 2.61$ and $H'_{rep1} = 2.85$), while undisturbed enclosures (experiment 1: $H'_{rep2} = 1.87$ and $H'_{rep1} = 2.06$; experiment 2: $H'_{rep2} = 2.04$ and $H'_{rep1} = 2.25$) and those disturbed every second day had a low diversity (experiment 1: $H'_{rep2} = 1.56$; experiment 2: $H'_{rep1} = 1.93$). Similarly, species number peaked at intermediate disturbance intervals: at 6-d intervals in experiment 1 ($n_{rep2} = 32$ and $n_{rep1} = 35$) and at 8-d intervals ($n_{rep2} = 48$ and $n_{rep1} = 53$) and 10-d intervals ($n = 50$) in experiment 2. (Subscripts indicate replicate treatments).

Conclusions

The significance of the response of diversity and species number was tested by multiple regression analysis (Table 2). Dependent variables were the diversity index (H') and the

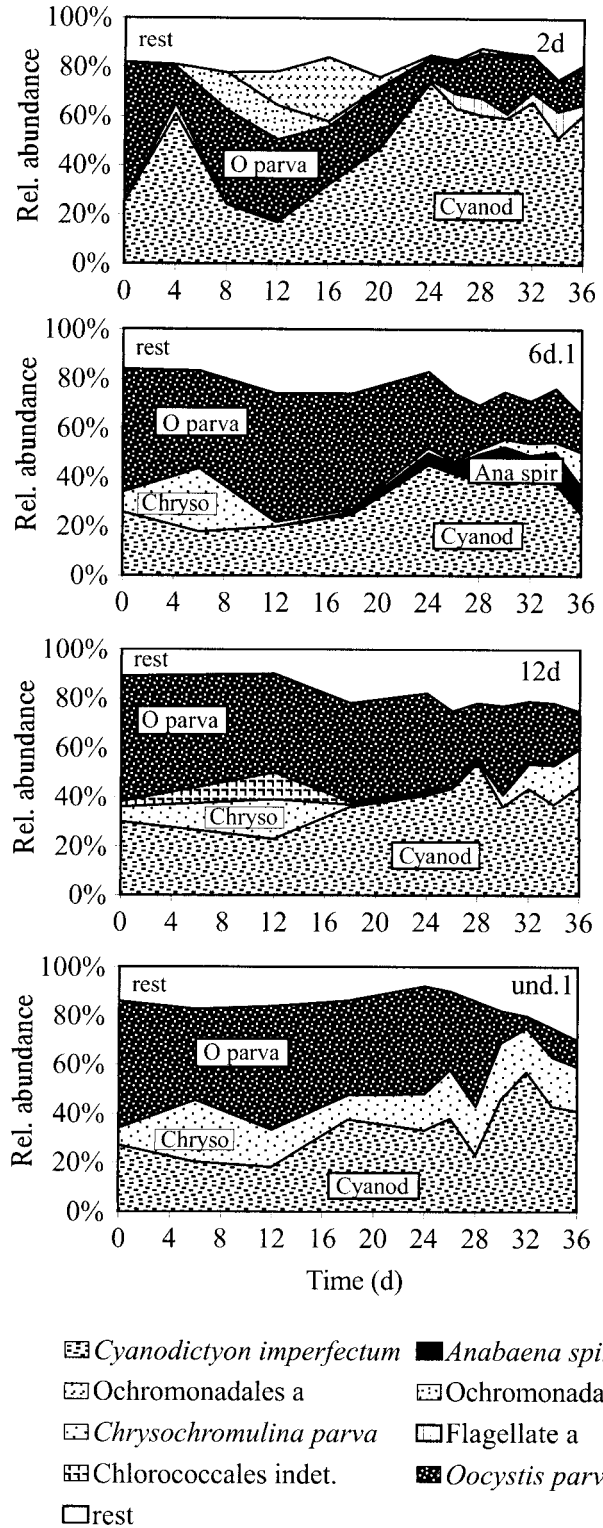


Fig. 3. Examples of the time course of phytoplankton abundance (based on organism density)—experiment 1: 2 d, 6 d, 12 d: length of the disturbance interval in days; und.: undisturbed treatment; \times .1: No. of the replicate. Mean between-replicate difference of dominant species was 21% (± 16.2 SD). Species that displayed an abundance of $>10\%$ at least once during the experiment are included. The other species are summarized as “rest.” Ana spir: *Anabaena spiroides*; Chryso: *Chrysochromulina parva*; Cyanod: *Cyanodictyon imperfectum*; O parva: *Oocystis parva*.

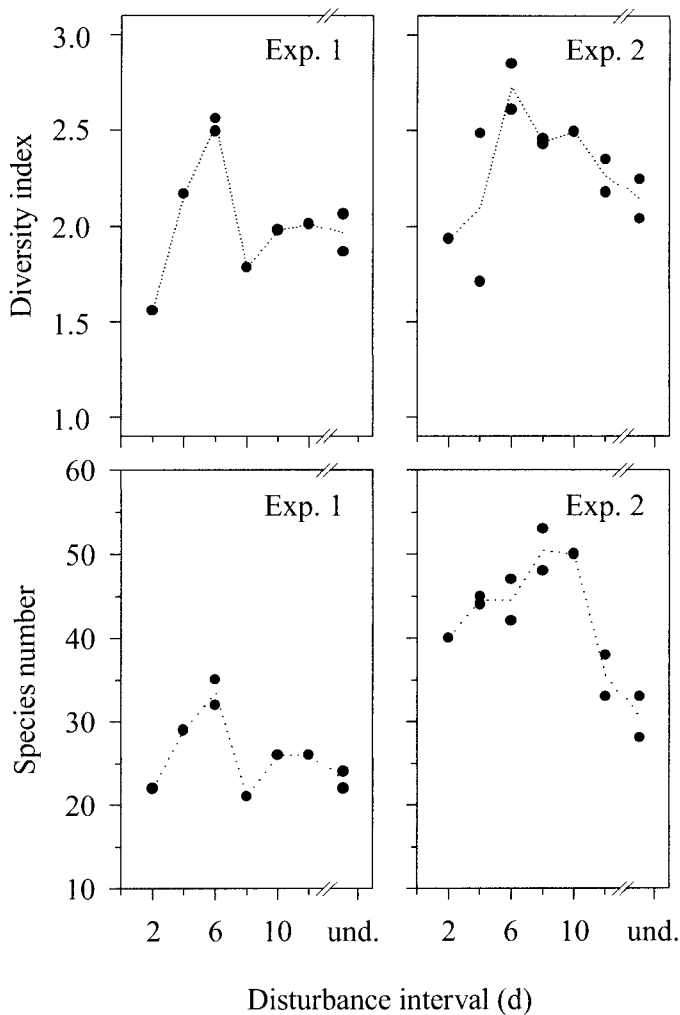


Fig. 4. Diversity index (H') and species number at the end of the experiments. 2–12 d: length of the disturbance interval in days; und.: undisturbed treatment. The dashed lines serve to provide orientation only. The higher value of H' and species number corresponds to the replicate $\times 1$ of the former figures. Experiment 1: 225% increase of the natural mixing depth (4 m); experiment 2: 150% increase of the natural mixing depth.

species number (S). Independent variables were the frequency of disturbance (F ; disturbance d^{-1}), intensity of nutrient disturbance (I), intensity of light disturbance (L), mean abundance of calanoid copepods, and mean abundance of *Daphnia*. Since the predicted relationship is nonlinear (Connell 1978), the squares of the independent variables were included. To confirm the IDH, there should be a unimodal response to the variables expressing frequency and intensity of disturbance (Sommer 1995). Linear terms should be significantly positive and quadratic terms significantly negative. Statistical analysis revealed highly significant correlations between both H' and S with some of the independent variables tested. The predictions of the IDH were confirmed when H' was used as the response variable. There was a unimodal response to F and I . The IDH was only partially confirmed when S was the dependent variable. A unimodal response was detected to F but not to the intensity of disturbance. It should be noted, however, that the experimental design was not particularly powerful in detecting the expected response to disturbance intensity. There were only two treatment levels that led to the variability of nutrient disturbance within the experiments because there were different nutrient effects in different enclosures. Both H' and S were influenced by *Daphnia* abundance. L affected the H' .

The results of these enclosure experiments are in close agreement with those found in the laboratory experiments of Gaedeke and Sommer (1986) and Sommer (1995), in which peaks in diversity were found when disturbance occurred every seventh day. The results also agree with Reynolds' (1988) suggestion that disturbances cause physiological responses if frequencies are in the order of a few hours (less than one generation time) but that larger disturbance intervals (10 d or more) can initiate a successional sequence. Environmental variability at intermediate time scales (20–200 h) interacts with growth rates and thus tends to preserve species diversity. There is a difference between the interval length that resulted in the highest diversity found in this study and that of Robinson and Sandgren (1983), in which a peak in H' occurred when the disturbance interval was 28 d, although maximum species numbers occurred under disturbance at 7-d intervals. The differences were probably caused by the different dilution rates of the chemostat sys-

Table 2. Multiple regression analysis with a stepwise variable selection (backward procedure, F to remove = 4). Dependent variables: H' , diversity index; S , species number. Independent variables: F , frequency of disturbance (disturbance d^{-1}); I , intensity of nutrient disturbance as change in concentration of the limiting nutrient phosphorus (%); L , intensity of light disturbance as mean deviation of light intensity (%) in epilimnion; DA , mean of *Daphnia* abundance (m^{-2}). Sign (β) and P level are of regression coefficient and equation of the regression.

Dependent variable	F	I	L	DA	F ²	I ²	L ²	DA ²
H'^*								
β	+	+	-		-	-	+	+
P level	0.0158	0.0008	0.0034		0.0069	0.0005	0.0039	0.0186
S^\dagger								
β	+			+	-			
P level	0.0087			0.0012	0.0216			

* $H' = 1.89 + 5.11 F - 10.19 F^2 + 0.01 I - 0.24 \cdot 10^{-4} I^2 - 0.44 L + 0.04 L^2 + 0.61 \cdot 10^{-10} DA^2$; $R^2 = 0.804$; $P < 0.0009$.

† $S = 15.96 + 99.05 F - 164.38 F^2 + 0.24 \cdot 10^{-3} DA^2$; $R^2 = 0.596$; $P < 0.0013$.

tems. At steady state, lower dilution rates result in longer generation times. When using the mean generation time as a yardstick for the interval length between disturbances, a striking similarity appears between all phytoplankton experiments in the laboratory: diversity peaks at disturbance intervals of 2–4 generation times.

There is evidence for the applicability of the IDH from empirical benthic studies (Aronson and Precht 1995; Townsend et al. 1997). However, a number of limnological field studies (Padisák et al. 1993) have documented the increase in phytoplankton diversity at intermediate frequencies of disturbance, but they lacked convincing examples for the reduction of diversity at high frequencies. Our experimental test of the IDH shows the increase of diversity following a disturbance regime of intermediate frequency and intensity. It also shows for the first time (under field conditions) a decrease in phytoplankton diversity when high frequencies of disturbance occur. This indicates that during the summer stratification phase of a dimictic lake, the IDH is a powerful tool for explaining the maintenance of a phytoplankton diversity that is higher than would be expected, according to the competitive exclusion principle (Hardin 1960). Thus, the IDH may contribute toward solving the paradox of the plankton (Hutchinson 1961).

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