

Phytoplankton community assembly in a large boreal lake – deterministic pathways or chaotic fluctuations?

JANNE SOININEN,* PETRA TALLBERG[†] AND JUKKA HORPPILA*

*Department of Biological and Environmental Sciences, University of Helsinki, Helsinki, Finland

[†]Finnish Environment Institute, Research Department, Helsinki, Finland

SUMMARY

1. The concepts of community assembly and succession are closely related, yet their foci differ slightly. Succession describes the trajectory of species replacements during the temporal development of the community, while assembly also allows that a locality can harbour different communities depending on the events in the near past of community development.
2. The aims of this study were (i) to examine the year-to-year variation in phytoplankton community assembly among basins of different trophy and disturbance in the large boreal Lake Hiidenvesi and (ii) to assess community persistence and diversity among basins in relation to prevailing environmental factors.
3. The results showed that the assembly did not follow similar trajectories each year. According to mean similarity analyses, there was a large degree of variability especially among the groups of samples collected in the same months of different years. Similarity between pairs of consecutive samples was highest in a cold year (1998) in all basins. Community assembly was most unpredictable in the basin of highest productivity, perhaps implying that the number of alternative stable states increased towards higher productivity. Our data also showed a strong unimodal relationship between phytoplankton species richness and grazing by cladoceran zooplankton in the basin of highest trophy.
4. This study showed that phytoplankton community assembly exhibited large variability among the years. This implies that different environmental conditions might be the strongest mechanism behind this pattern, given that the degree of community similarity paralleled the year-to-year variation in mean temperature. Unravelling the patterns in community assembly has a number of important implications, especially for the monitoring of ecological impacts based only on snapshots of biological assemblages.

Keywords: alternative stable states, assembly, persistence, plankton, productivity

Introduction

Temporal changes in community structure (i.e. assembly or succession) have long attracted the attention of ecologists. The concepts of community assembly and succession are closely related, yet they have slightly

different foci (Chase & Leibold, 2003). Succession focuses on the trajectory of species replacements during community development, while assembly concentrates more on the end state of community structure and its diversity. Moreover, community assembly allows for the possibility that the same locality can harbour different communities depending on the events in the near past of community development, (e.g. invasions from the regional species pool) leading to a spectrum of alternative stable states

Correspondence: Janne Soininen, Department of Biological and Environmental Sciences, University of Helsinki, P.O. Box 65, FIN-00014, Helsinki, Finland. E-mail: janne.soininen@helsinki.fi

(Chase, 2003). Chase (2003) stressed the role of disturbances, productivity, size of the regional species pool and connectivity as major factors in determining whether community assembly would lead to a single or multiple stable equilibria. For closely located sites sharing the same regional species pool, the role of disturbance and productivity may be especially influential.

Disturbance is one of the most influential factors affecting community structure (Sousa, 1984; MacKey & Currie, 2001), and Connell (1978) stressed that disturbances of intermediate strength and frequency maintain high diversity in communities, widely known as the Intermediate Disturbance Hypothesis. Effects of disturbance on assembly, stability and diversity of biological communities depend, however, on the life span and size of community residents. For example, microscopic organisms, such as most of the algae, are disrupted by a high proportion of disturbance events (Townsend, Doledec & Scarsbrook, 1997), often leading to rapid and severe changes in community structure. Like disturbances, primary productivity is considered to be a major determinant of species composition and diversity in most ecosystems (e.g. Waide *et al.*, 1999). Disturbance intensity and frequency, whatever their nature, combined with the variation in primary productivity should thus often provide the most important drivers of community properties.

A lake comprised of basins with substantially different degree of trophicity and susceptibility to disturbances should provide a suitable model system to examine whether the dissimilarity of community composition of successive samples increases along both the productivity and disturbance gradients. According to Chase (2003), community assembly should be most predictable, or lead to a single stable equilibrium, in environments with low productivity and high disturbance. Moreover, Steiner & Leibold (2004) suggested that the assembly processes that lead to repeated cyclical changes in composition, rather than a few composition endpoints, are more likely at high productivity. In low productivity environments, only a limited number of species can persist, and interaction between resource competition and competition mediated through predators or grazers can lead to more frequent multiple stable equilibria at high than at low productivity (Chase & Leibold, 2003). Moreover, localities with higher rates of disturbance

are less likely to exhibit multiple stable equilibria because only a subset of species can persist, or frequent disturbances will prolong the time for an early colonising species to attain high abundance (Chase, 2003). Consequently, according to our conceptual model (Fig. 1), multiple stable equilibria should be more common in the most productive basin (Kirkkojärvi) of Lake Hiidenvesi, and by contrast, community assembly should be most predictable in the basin with lowest productivity (Kiihkelyksenselkä). However, due to natural properties of the lakes, basins with highest productivity are usually also the most susceptible to disturbances because of their shallowness, and the number of stable equilibria may be difficult to associate unequivocally with either productivity or disturbance. However, we predict, that the level of productivity is a more dominant driver in our study system, given that the metalimnion of the lake is aphotic because of high inorganic turbidity. A small study extent and high connectivity between the adjacent basins should ensure that the basins share the same algal species pool because of continuous dispersal of the cells among basins.

The specific aims of this study were first (i) to examine the year-to-year variation in phytoplankton community assembly among basins of different trophicity and disturbance in the large boreal Lake Hiidenvesi. Specifically, we examined whether community assembly followed deterministic pathways or was

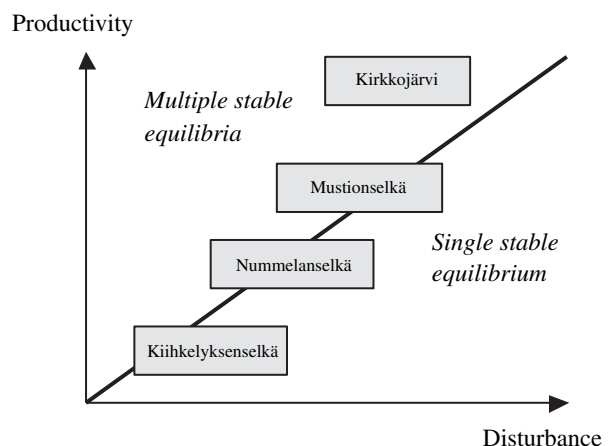


Fig. 1 A conceptual model of hypothesised locations of the four studied basins of Lake Hiidenvesi in relation to their productivity and susceptibility to disturbances (depth). See Methods and Chase (2003) for further details.

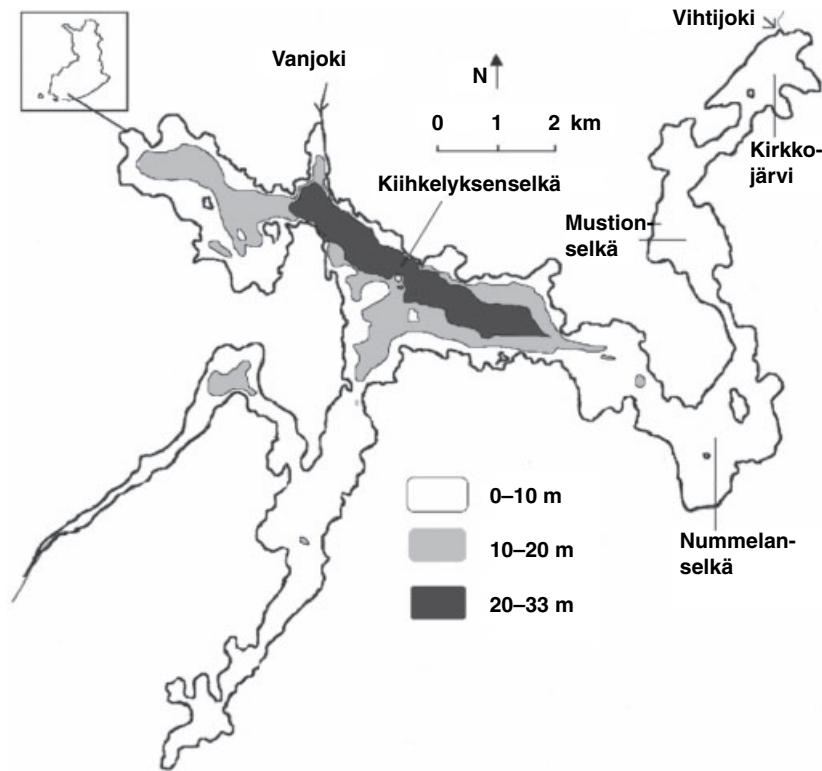


Fig. 2 Map of Lake Hiidenvesi and its four basins located in Southern Finland.

characterised by variation in invasion sequences from a regional pool. We hypothesise that the year-to-year variation will be larger in more productive basins than in basins with the lower productivity. Secondly, (ii) our purpose was to assess phytoplankton community persistence and diversity in relation to a number of environmental factors. There is a dearth of studies addressing the diversity–disturbance relationship in relation to multiple disturbance mechanisms. Therefore, together with physical disturbances, the role of a biotic disturbance, namely variation in cladoceran zooplankton grazing pressure, was also examined.

Methods

Study area and sampling

Lake Hiidenvesi, which is located in southwestern Finland (60°24'N, 24°18'E) (Fig. 2), has a surface area of 30.3 km² and consists of several separate basins. The lake has for decades suffered from eutrophication because of external nutrient loading. The lake is also clay-turbid because of resuspended sediments and

external loading of inorganic suspended solids. Samples for water chemistry, phytoplankton and zooplankton were taken every 2 weeks (9:00–15:00 hours) from 1997 to 2001 from the deepest point of each of the four main basins (Kirkkojärvi, Mustionselkä, Nummelanselkä and Kiihkelyksenselkä, Fig. 2). Non-stratifying Kirkkojärvi basin (area 1.6 km², mean depth 1.1 m, max 3.5 m) and Mustionselkä basin (area 2.7 km², mean depth 1.7 m, max 4.5 m) represent the most eutrophic parts of the lake, with total phosphorus (P) concentrations ranging from 70 (Mustionselkä) to 90 µg L⁻¹ (Kirkkojärvi). Because of the high concentration of inorganic suspended solids and frequent algal blooms, surface water turbidity often exceeds 40 NTU and the Secchi depth usually remains below 0.5 m (Tallberg *et al.*, 1999; Niemistö, Tallberg & Horppila, 2005). Nummelanselkä basin (area 3.8 km², mean depth 2.5 m, max 7.0 m) may be temporarily stratified during calm weather. In Nummelanselkä, the total P concentration usually fluctuates around 50 µg L⁻¹ and the Secchi depth between 0.5 and 1 m. Kiihkelyksenselkä basin, which is the largest and deepest basin of the lake (area 10.5 km², mean depth 11.3 m, max 33.0 m), is perma-

nently stratified during the summer months and its total P concentration is usually *c.* 40 µg L⁻¹, the epilimnetic turbidity values are below 20 NTU and the Secchi depth of around 1 m. The characteristics of the different basins have been described in more detail in Tallberg *et al.* (1999); Horppila (2005) and Niemistö *et al.* (2005).

Samples for water chemistry and zooplankton were hauled with a tube sampler (*h* = 1 m, *V* = 7.5 L) from each metre and pooled into one sample in Kirkkojärvi (water depth 3 m), Mustionselkä (4 m) and Nummelanselkä (6 m). In Kiihkelyksenselkä (30 m), the samples were combined into six separate layers (0–5, 5–10, 10–15, 15–20, 20–25 and 25–28 m). Water temperature, total P, total N concentrations and dissolved oxygen were also measured at each sampling station using methods described in Tallberg *et al.* (1999). Samples for phytoplankton were taken from the epilimnion (0–2 m) with a tube sampler and preserved with acid Lugol's solution. Phytoplankton samples were counted using the inverted microscope technique (Utermöhl, 1958). A minimum of 10 cells from each of the dominant species were measured and the cell numbers were converted to biomass using stereometric equations (Edler, 1979). Zooplankton samples were filtered through a 50 µm net and preserved with formaldehyde. Thirty individuals from each taxon were measured. Daphnids were measured from the centre of the eye to the base of the tailspine, and other species from the anterior edge of the carapace to the posterior edge. Individual biomasses were calculated using length-carbon regressions (Tallberg *et al.*, 1999). Data on wind speed (eight measurements per day, averages over 10 min each) were obtained from the airport situated 40 km east of Lake Hiidenvesi.

Data analysis

Phytoplankton taxa occurring in at least two samples were included in the statistical analyses, thus giving total of 113 taxa in Kirkkojärvi, 124 taxa in Mustionselkä, 119 taxa in Nummelanselkä, and 80 taxa in Kiihkelyksenselkä. Non-metric Multidimensional Scaling (NMDS) was used to describe temporal variation among phytoplankton community structure. Specifically, using the NMDS-ordination we assessed whether the community assembly followed similar trajectories

among the years of this study period. NMDS is highly suitable for ecological data containing numerous zero values (Minchin, 1987). To reduce the chance of local optima, 10 random starts were carried out. The one with the lowest stress value was used as starting coordinates for the analysis. A two-dimensional solution was chosen, as stress values changed only slightly with subsequent dimensions. Sorensen's distance measure was used for the analysis. The statistical significance of differences between the community compositions among sampling years or among samples of different sampling months irrespective of the year was tested using Multi-Response Permutation Procedures (MRPP; Berry, Kvamme & Mielke, 1983; Biondini, Bonham & Redente, 1985). This is a non-parametric procedure for testing the significance of possible differences between *a priori* classified groups. MRPP has the advantage of not requiring assumptions such as multivariate normality and homogeneity of variances and is easily applied to multivariate space. Within-group homogeneity was evaluated using chance-corrected within-group agreement *A*. If the value of *A* is >0, the within-group homogeneity is larger than expected by chance. NMDS and MRPP were performed using the program PC-ORD version 4 (McCune & Mefford, 1999). The classification strength (CS) of sampling years and months was tested using the randomisation protocol of Van Sickle & Hughes (2000). The mean of all between-group similarities (*B*) and the within-group mean similarity (*W*) were first calculated using Sorensen similarity coefficient. CS is defined as the difference between these similarities (CS = *W*–*B*). Values of this measure range from 0 to 1, with those near zero indicating that samples are randomly assigned to groups. The observed values of CS were compared with permuted values, obtained through 1000 random reassignments of samples to groups. However, such permutation tests, are known to be too powerful (i.e. even very small differences between observed and expected values of CS are statistically significant, if sample size is moderately large). We therefore followed the recommendation of Van Sickle & Hughes (2000) to place most emphasis on comparisons of the relative magnitude of CS statistic than on the *P*-values from the randomisation tests.

Regression analysis was used to relate the changes in community structure with corresponding changes in environmental conditions, i.e. water chemistry and

mean wind speed. We used Jaccard-similarity measures:

$$J(AB) = \frac{j}{(a + b - j)},$$

where a is the number of taxa in community A (first sample in any pair), b is the number of taxa in community B (the second sample in any pair) and j is the number of taxa found in both communities. Finally, monthly changes in species composition or percentage turnover (T) were used to indicate community persistence. Turnover was calculated as

$$T = \frac{(G + L)}{(S_1 + S_2) \times 100},$$

where G and L are the number of taxa gained and lost between the sampling occasions, and S_1 and S_2 are number of taxa present in successive sampling occasions (Diamond & May, 1977; Brewin, Buckton & Ormerod, 2000). Regression analysis was also used to examine the relationship between changes in phytoplankton diversity and mean wind speed. Furthermore, we tested whether the observed high phytoplankton diversity could be accounted for by biotic disturbances of intermediate intensity. Thereby, variation in grazing pressure by zooplankton was studied (see also Eloranta, 1993). Grazing was calculated from cladoceran zooplankton biomass (Z) according to Lampert (1988): $Z = 83$ mg C per gram dry weight per day.

Results

Phytoplankton communities differed more in terms of community composition among the sampling years than among the months, irrespective of the year in NMDS ordination space (Fig. 3). In the year 1997 with the highest mean temperature (Fig. 4), phytoplankton communities were highly specialised excluding the stratified Kiihkelyksenselkä, where community structure differed substantially from the rest of the study years in 1999. Although differences between the *a priori* groups (i.e. groups of all samples of the same year or all samples of the same sampling month irrespective of the year) were significant according to MRPP (all $P < 0.01$), within-group agreements (A) were higher among groups of samples collected in the same year (Fig. 3). Also according to CS, groups of all samples of the same year showed higher specialisation; that is, higher CS values than groups of samples

of the same sampling month (Fig. 3). The community assembly was most predictable, i.e. had the highest CS (0.079) in Kiihkelyksenselkä, and was most variable in Kirkkojärvi, with the lowest CS (0.024).

Similarity between pairs of consecutive samples was highest in the cold year of 1998 in all basins (Fig. 5). However, according to multiple linear regression analyses, these data did not show any significant relationship between community similarity of consecutive samples and corresponding changes in environmental conditions. Phytoplankton species richness also fluctuated substantially in all basins, communities being more diverse after diatom maximum abundance in spring (Fig. 5). In the warm years of 1997 and 1999, substantial blue-green algal blooms (e.g. *Anabaena spiroides* and *Microcystis* sp.) were reflected as notably depauperate communities, especially in basins of higher productivity. For detailed description of phytoplankton communities, see Tallberg *et al.* (1999).

There was a significant positive relationship between mean temperature and average species turnover among years ($r = 0.829$, $P < 0.05$). Phytoplankton communities were characterised by high temporal variability among successive samples. On average, species turnover between the consecutive samples was highest in Mustionselkä (mean turnover 46.6%) and lowest in Kirkkojärvi (mean turnover 38.0%) (Table 1). The high degree of species turnover that phytoplankton exhibited was also reflected in occurrence frequency distribution of phytoplankton assemblages. This showed a clear satellite-mode; that is, the proportion of satellite species (species present in <30% of samples) was high compared with that of core-species (Table 1). Among the basins, the number of satellite species was lowest in Kirkkojärvi.

When assessing the diversity–disturbance relationship, mean wind speed and phytoplankton diversity did not show any significant relationship. Yet, there was a strong unimodal relationship between phytoplankton species richness and grazing by cladoceran zooplankton in Kirkkojärvi (Fig. 6, Table 2). However, these data did not show any significant relationships between zooplankton grazing intensity and phytoplankton species richness in other basins.

Discussion

Our data showed that phytoplankton community assembly does not follow similar trajectories each

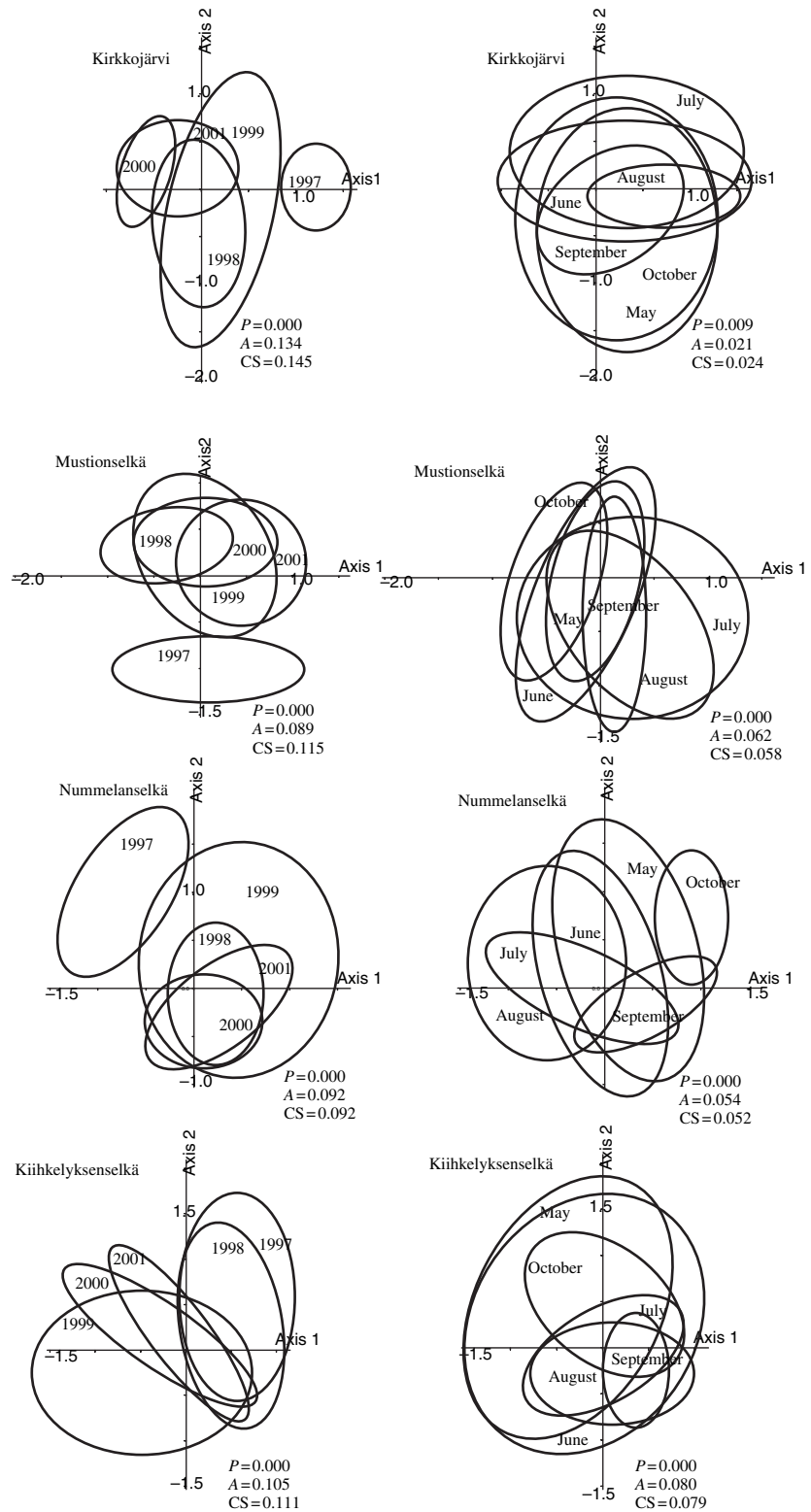


Fig. 3 Ordination diagrams for Non-metric Multidimensional Scaling analyses of phytoplankton communities sampled in years 1997–2001 in four basins of Lake Hiidenvesi. Column on the left hand side consists of figures where samples collected in same years are enclosed by ellipses, while column on the right hand side consists of figures where samples representing the same months, irrespective of the year, are enclosed by ellipses. The results of Multiresponse Permutation Procedures (MRPP) and classification strengths (CS) are also shown. In MRPP, the null hypotheses of no differences among groups (years or months) were assessed using a Monte Carlo permutation procedure with 1000 permutations. A is the within-group agreement. In CS analysis, the test statistic was obtained by subtracting the mean of all between-group similarities from the within-group mean similarity. Thus, the higher the CS -value, the higher is the within-group similarity compared with between-group similarity. Figures on axes represent the standard deviations of community data.

year. According to mean similarity analyses, there was a large degree of variability especially among the groups of samples collected in the same months, but

in different years. Moreover, according to within-group agreements it was evident that community composition showed higher similarity within

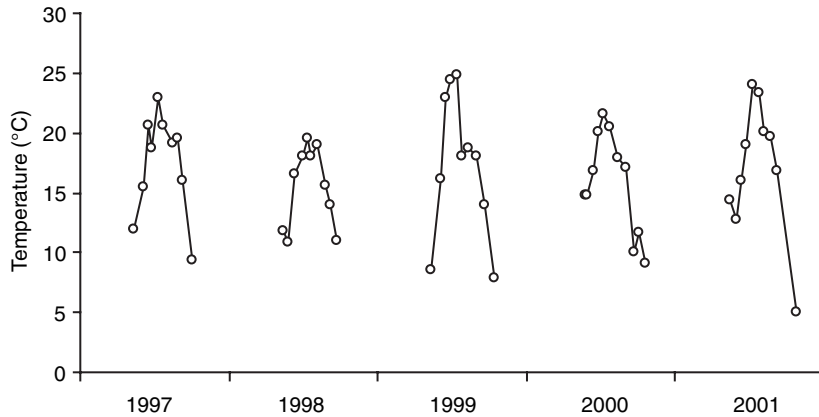


Fig. 4 Water temperatures in Lake Hiidenvesi (Kirkkojärvi) during 1997–2001. Numbers refer to mean temperatures during the phytoplankton sampling each year.

sampling years than within sampling months, irrespective of the year. This implies that different environmental conditions might be the most influential in different years, given that the levels of community similarity largely paralleled the year-to-year variation in mean temperature. Temperature also played a large role in affecting the level of species turnover between successive samples; there was a significant relationship between annual mean species turnover and annual mean temperature. Given that the time between cell divisions declines as temperature increases, this could simply arise from temperature dependent growth-rate, thus leading towards higher dissimilarity of consecutive samples at higher temperature. These findings are therefore congruent with the results by Sommer (1991) and Weiher & Keddy (1995), who stressed the role of environmental factors, and thereby, species competitive interactions in regulating community assembly.

Temperature-dependent growth rate and associated patterns, are crucial in determining the structure of biological communities. Processes are reflected in community properties, their local (α -) and regional (γ -) diversity, and perhaps most importantly, variation in species composition (β -diversity) across multiple scales. Corroborating the predictions by Chase (2003) and Steiner & Leibold (2004), community assembly was most unpredictable, (i.e. communities were most distinctive among the years) in the basin of highest productivity, perhaps implying that the number of alternative stable states increases towards higher productivity. This general prediction concurs with empirical data gathered earlier for various freshwater organisms in ponds (Chase & Leibold, 2002, 2003). In our study system, the pattern could

result from a larger capacity to form blue-green algal blooms in basins of highest productivity, as shown in terms of a highly specialised blue-green dominated community especially in the warm year of 1997. Also, given that zooplankton grazing affected phytoplankton diversity in the basin of highest productivity, interaction between resource competition and competition mediated through grazers could have led to a higher number of equilibria (Chase, 2003). The primary reason why susceptibility to disturbances was probably not a major driver in our system may be attributed to severe light limitation, even in the epilimnion, because of high inorganic turbidity, thus leading only to relatively subtle variability in light intensity along the disturbance gradient. The lack of significant relationship between mean-wind speed and phytoplankton diversity in Lake Hiidenvesi also lends support to this argument.

As also reported in other papers addressing the persistence and stability of various organisms in freshwater ecosystems (Duncan & Blinn, 1989; Scarsbrook, 2002; Soininen & Eloranta, 2004), there were no significant relationships between short-scale variability in environmental parameters and corresponding dissimilarities in community structure. Moreover, although year-to-year variability in community assembly was highest in Kirkkojärvi, phytoplankton communities showed the lowest seasonal species turnover in this basin. While this may at first glance seem counterintuitive, it probably reflects the fact that communities were dominated by relatively long-lasting blue-green blooms throughout the main part of the summer. Besides temporal community development, we also tested the Intermediate Disturbance Hypothesis (Connell, 1978) using mean wind

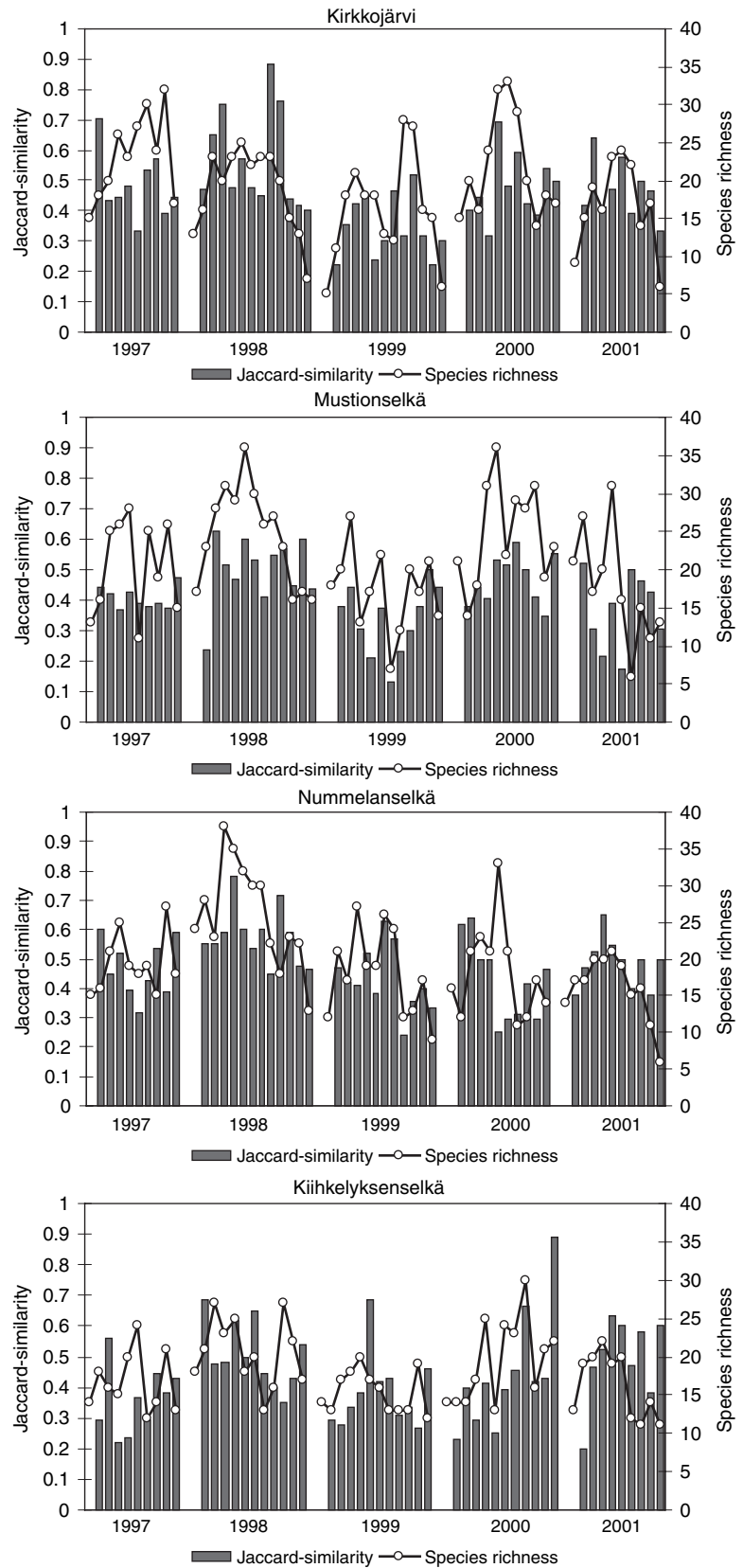


Fig. 5 Phytoplankton species richness and persistence in years 1997–2001 in four basins of Lake Hiidenvesi. Persistence was indicated by values of Jaccard-similarity between consecutive samples.

	Kirkkojärvi	Mustionselkä	Nummelanselkä	Kiihkelyksenselkä
Year	Species turnover (%)			
1997	33	46	48	52
1998	34	38	33	40
1999	45	52	46	41
2000	39	43	45	44
2001	39	54	40	37
Satellite class (%)	Percentage of species in class			
<10	42	52	56	50
10–19.9	26	26	22	25
20–29.9	16	7	11	10

Table 1 Phytoplankton species turnover and proportion of satellite species (species which occur in <10%, 10–19.9% and <30% of samples) in four basins of Lake Hiidenvesi in years 1997–2001. Species turnover (%) was calculated as $T = (G + L)/(S_1 + S_2) \times 100$ where G and L are the number of taxa gained and lost between sampling occasions, and S_1 and S_2 are number of taxa present on successive sampling occasions.

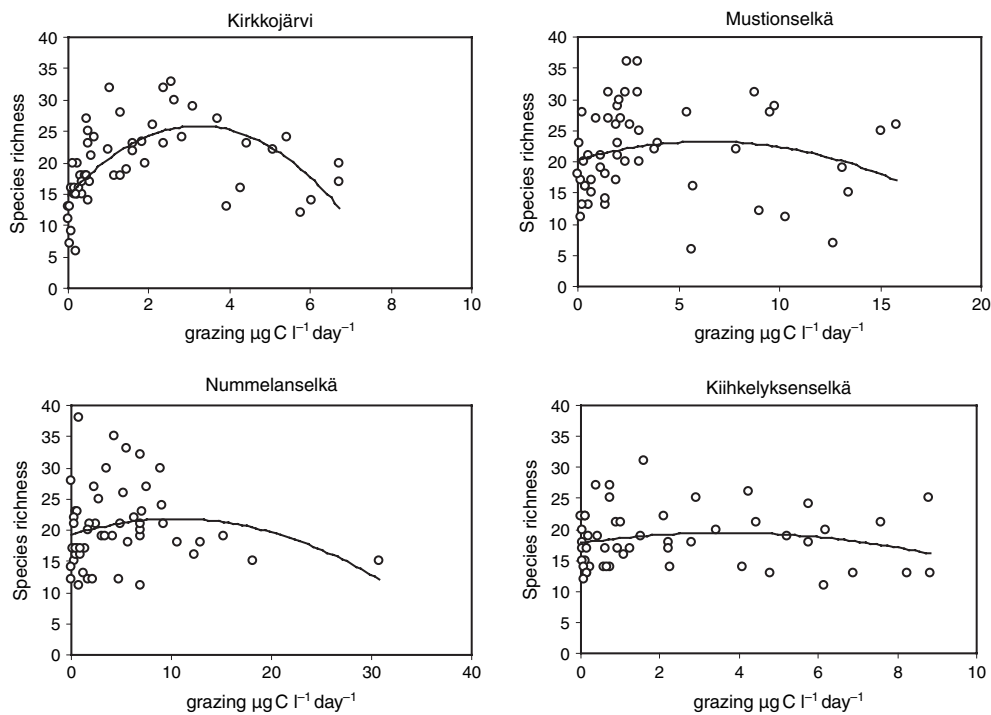


Fig. 6 The relationship between phytoplankton species richness and grazing pressure by cladoceran zooplankton in four basins of Lake Hiidenvesi. The models that best fit to data are shown.

speed and zooplankton grazing as a proxy for physical and biological disturbances, respectively. As concluded in a number of earlier studies (e.g. Rojo & Alvarez Cobelas, 1993) mean wind speed and phytoplankton diversity were not significantly related, thus showing the complexity of plankton dynamics (but see Grover & Chrzanowski, 2004). However, there are, some important conclusions to make. The unimodal relationship between phytoplankton species richness and grazing by cladocerans

was notably strong in the basin of highest productivity. The stronger effect of cladocerans on phytoplankton in Kirkkojärvi compared with other basins was probably because of among-basin differences in species composition of the cladoceran assemblage. Among different cladoceran taxa, daphnids are known for their ability to consume particles in a wide size range (Lampert, 1987), extending the effect of grazing to the whole phytoplankton community. In Kirkkojärvi, the highest observed grazing rates could

Table 2 Regression models relating phytoplankton species richness (SR) to mean wind speed and grazing by cladoceran zooplankton

		d.f.	P	R ²
SR versus mean wind speed	Linear	223	n.s.	0.023
	Quadratic	223	n.s.	0.023
SR versus grazing Kirkkojärvi	Linear	50	n.s.	0.042
	Quadratic	50	<0.0001	0.394
Mustionselkä	Linear	51	n.s.	0.001
	Quadratic	51	n.s.	0.029
Nummelanselkä	Linear	50	n.s.	0.003
	Quadratic	50	n.s.	0.050
Kiihkelyksenselkä	Linear	51	n.s.	0.000
	Quadratic	51	n.s.	0.031

be accounted for by the high abundance of daphnids (Horppila *et al.*, 2005), and coincided with the dominance by large-sized algae and low algal diversity. During periods of low abundance of daphnids and low grazing, phytoplankton was dominated by small-sized cryptomonads, whereas at intermediate grazing rates, high algal diversity prevailed. Such shifts in phytoplankton size structure have been attributed to variations in the zooplankton assemblage and may be due to variable grazing capabilities of different zooplankton taxa (Peters & Downing, 1984; Bergquist, Carpenter & Latino, 1985).

Succession in phytoplankton communities has been well studied in freshwater ecosystems using intensive sampling, but mainly from the perspective of the dynamics of individual populations or different algal groups (for theory, see Sommer *et al.*, 1986). This paper is meant to provide further understanding of the community-level patterns in assembly (see also Law & Morton, 1993, 1996; Jenkins & Buikema, 1998), as well as phytoplankton persistence and diversity. Community assembly has many important implications for biodiversity conservation as well as for long-term bioassessment programs. One of its most novel implications is that local communities of species-rich regional pools are 'tested' against a very large number of potential invaders from the pool; this should maintain localities with large regional species pools highly resistant to invasions, thus leading to the conclusion that regional biodiversity does matter (Law & Morton, 1996). The second important implication is connected with monitoring of ecological impacts. Bioassessment and conservation programs

are usually based on single observations; information obtained by such discrete 'snapshots' should be rigorously assessed to confirm their usability and cost-effectiveness as a base in long-term bioassessment programs. Ultimately, community assembly affects the diversity of local communities. Besides being worthwhile for conservation in itself, negative consequences of biodiversity loss on ecosystem functioning have become increasingly debated among conservation biologists (e.g. Vitousek *et al.*, 1997).

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