Temporal and spatial heterogeneity of pelagic plankton in Lake Pyhäselkä, Finland

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Phytoplankton and zooplankton constitute a cascade in which relationships and the behavioural strategies of organisms are involved in complex and dynamic ways on various temporal and spatial scales. In this study, we used a combination of short-interval sampling and spatial data analysis to investigate the distribution patterns of pelagic phyto- and zooplankton in Lake Pyhäselkä, a moderately large (263 km^2) mesotrophic and humic lake in eastern Finland. The general goal of this work was to improve our understanding of pelagic plankton interactions and dynamics in large lakes. The specific objective was to reveal and verify the short-interval day-to-day temporal and spatial distribution patterns of pelagic plankton in 2005 in Lake Pyhäselkä. We can conclude from our results that phytoplankton and zooplankton exhibit seasonally and spatially heterogeneous distribution; the most obvious differences in phytoplankton and zooplankton abundance and biomass, and in the water quality parameters, were seasonal ones, and these were statistically highly significant; there were obvious small-scale, short-interval day-to-day variations in temperature and the horizontal and vertical distribution of phytoplankton and zooplankton; and the validity of a comparative inter-lake approach and long term monitoring of one lake would greatly depend on the question of whether the samples had been taken in the same month, at the same place and at comparable points in the vertical water column.

Introduction

Spatial heterogeneity is a common feature of ecosystems and is the product of many inter-acting physical, chemical and biological processes (Pinel-Alloul 1995). Recognition of the importance of spatial and temporal scales is a relatively recent issue in ecological research

into food webs (Bertolo *et al.* 1999, Woodward and Hildrew 2002, Bell *et al.* 2003, Mehner *et al.* 2005). The spatial distribution of plankton is usually highly aggregated (George 1981, Malone and McQueen 1983, Urabe 1990, Viljanen and Karjalainen 1993, Carter *et al.* 1995, Karjalainen *et al.* 1996a), densities being mainly controlled by the feeding regimes of planktivorous fish (Sarvala *et al.* 1998). Information on the simultaneous distributions of organisms at different trophic levels in the food web, combined with physical and chemical information, constitutes the basic material for modelling a pelagic ecosystem (Carpenter 1988, Benndorf 1990, Gulati *et al.* 1990, Mallin and Paerl 1994, Karjalainen *et al.* 1996a, Sarvala *et al.* 1998, Pace *et al.* 1999, Jeppesen *et al.* 2003, 2005a, 2005b).

On large spatial scales, physical processes such as wind (Jones *et al.* 1995), wind-induced currents (Lacroix and Lescher-Moutoue 1995, George and Winfield 2000, Thackeray *et al.* 2004, Rinke *et al.* 2007), water temperature and stability (Betsill and van den Avyle 1994, Pinel-Alloul *et al.* 1999) and inshore–offshore temperature gradients (Johansson *et al.* 1991, Stockwell and Sprules 1995) are thought to have a dominant influence on the spatial distribution of organisms, but on smaller scales there are various biological processes (predation, competition, swarming and avoidance behaviour, reproductive behaviour, size of plankton, food resources, etc.) that serve to decouple organisms from the direct effects of many physical processes (Legendre and Demers 1984, Pinel-Alloul *et al.* 1988, Wiens 1989, Johansson *et al.* 1991, Viljanen and Karjalainen 1993, Lacroix and Lescher-Moutoue 1995). The combined action of wind-induced water movements and organism behaviour can result in large-scale spatial heterogeneity (Thackeray *et al.* 2004). Also on small spatial scales, planktonic crustacea exhibit swarming behaviour initiated in the presence of predators (Jakobsen and Johnson 1987), which can reduce the feeding efficiency of visual predators (Milinski 1977) or reduce predator–prey encounter rates (Pinel-Alloul *et al.* 1988).

In this study, we set out to examine the spatial and temporal heterogeneity in the environment and plankton community of a moderately large lake. The aim was to reveal and verify the short-interval day-to-day temporal and spatial distribution patterns of pelagic plankton in Lake Pyhäselkä during the summer, and to analyse the influence of sampling time, place and depth on two biological variables (phytoplankton and zooplankton), two chemical ones (total phosphorous and nitrogen contents) and two physical ones (temperature and water colour).

One of the additional objectives was to produce data for a 3D hydrodynamic and ecological model application which would be based on the Coherens code (Luyten *et al.* 1999). This model has been used successfully to study vertical mixing in the Danish straits (Bendtsen *et al.* 2006). Ecological data for model calibration and validation, especially of phytoplankton fractions, is scarce, and the measurements in this study produce a sufficient dataset for the calibration and validation of the 3D model application.

Study area, material and methods

Lake Pyhäselkä is a moderately large (263 km^2) mesotrophic and humic lake in eastern Finland (Fig. 1). It forms a part of the Vuoksi river basin and has a catchment area of 1285 km^2. The mean depth of the lake is 9 metres, maximum depth 67 metres and volume 2.5 km^3. The theoretical water retention time is 3.5 months. The deep parts of the lake are situated in the middle, and the lake is open and almost without islands, so that it is sensitive to wind-induced currents. The Pielisjoki (mean discharge 228 m^3 s^{-1}) flows into the northern part of the lake and affects its physicochemical features.

Samples in this study were taken two times during the open water season: at the end of May–beginning of June and at the end of August. Sampling was focused on investigating short-interval day-to-day variations. Field sampling was performed on board r/v *Muikku*. Samples were obtained by repeating the same sampling programme three times on consecutive days. The sampling at each station was carried out at the same order and time of day between 9:00 and 18:30. Two stations, Kokonluoto and Pyhäsaari, were located in the deep, southern and central parts of the lake, and one, Noljakka, in the northern, loaded part (Fig. 1).
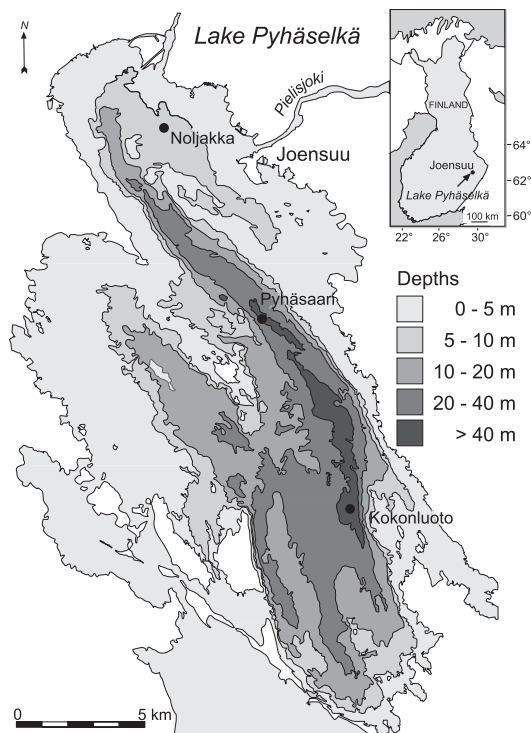
Fig. 1. Bathymetric map of Lake Pyhäselkä showing the locations of sampling stations.

Fig. 2. Seasonal and short-time day-to-day variations in temperature (°C) and fluorometer values (flu) at three sampling stations in Lake Pyhäselkä in 2005.

The samples for physical and chemical analyses (temperature, secchi depth, turbidity, colour, P_{tot}, PO_4-P, N_{tot}, NO_3-N, chlorophyll *a*) were taken at a depth of 1 metre, at a depth corresponding to the middle of the water layer and at a point just above the bottom. They were analysed by standard methods (Vesihallitus 1981). Samples were also compared and used for controlling the data of the CTD meter. Water stability was estimated from the vertical water density gradient using the Brunt-Väisälä frequency (e.g. *see* Apel 1987), and the theoretical period of oscillation for internal seiches with the method originally presented by Mortimer (1953).

Water temperature, conductivity, pH and chlorophyll fluorescence *in vivo* (Scufa) were measured with a Sea-Bird Electronic 19-03 CTD meter. The three consecutive measurements were made at each sampling station as vertical profiles from surface to bottom (Fig. 2). The coefficients of variation (CV%) between the ten consecutive CTD measurements varied from 0.001% to 3% for temperature and from 0.3% to 9% for fluorometer values.
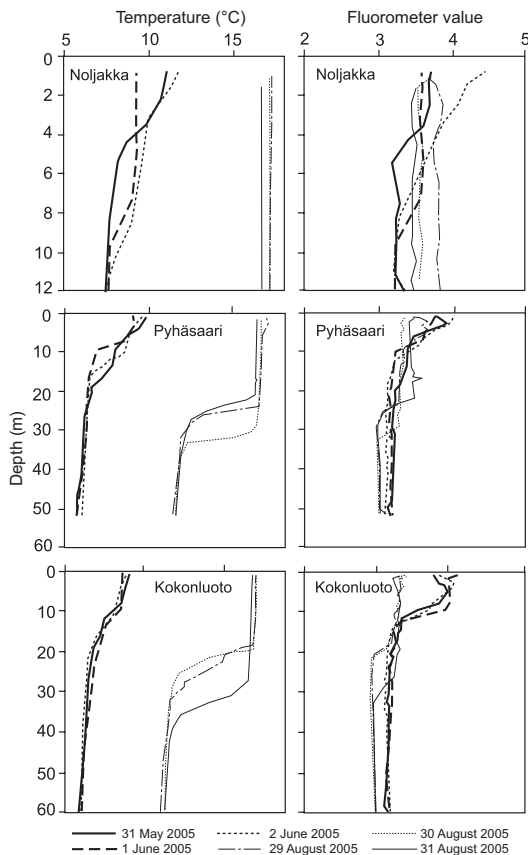
Samples for phytoplankton and chlorophyll *a* were taken with Limnos tube sampler and Rosette sampler at depths of 1, 5, 10, 20 and 40 metres. The phytoplankton samples were fixed with acid Lugols's solution, and the abundances of the taxa were determined with an inverted microscope using a settling chamber technique. The abundances of the dominant species were analysed: the Cryptophyceans *Cryptomonas* spp. and *Rhodomonas lacustris*, the diatoms *Aulacoseira distans*, *Aulacoseira* spp., *Tabellaria flocculosa* and *Asterionella formosa*, and the blue-green algae *Anabaena* sp. and *Aphanizomenon* sp. The biomass calculated in this way represented 26.4%–72.5% (mean = 46.9%) of the total biomass of the sample. The cell counts were converted to biovolumes using the cell volumes of the phytoplankton database of the Finnish Environment Institute. Phytoplankton biomasses

are given as fresh weight (mg l⁻¹). A fluorometer was used to estimate chlorophyll *a* and the abundance of phytoplankton on both temporal and spatial scales.

The zooplankton samples were collected from the depths of 1, 5, 10, 20 and 40 metres by means of a diaphragm pump, which treats the animals best and ensures that they will survive intact. The total volume of each sample was 100 l. The pump was connected to an in-line OPC (Optical Plankton Counter) system and a zooplankton sample was collected with a net of mesh size 50 μm immediately after the OPC. The samples were preserved in ethanol on board r/v *Muikku* and neutralized formalin was added in the laboratory. The sufficient number of well-mixed subsamples was taken with a pipette and the crustaceous zooplankton was counted in a sedimentation cuvette with an inverted microscope. The precision of the counting procedure had been tested earlier (Karjalainen *et al.* 1996b). The zooplankton densities were converted to biomass by reference to average carbon values for the size classes of each taxon (Rahkola *et al.* 1998).

The influence of sampling time, place and depth on two biological variables (phytoplankton and zooplankton), two chemical ones (total phosphorous and nitrogen contents) and two physical ones (temperature and water colour) was tested statistically. Samples taken from the depths of 1, 5 and 10 metres were included in all the data analysed, but samples from deeper water layers had been taken only at two stations (Pyhäsaari and Kokonluoto). Sampling times were divided into a short and a long interval,

one day and one month, respectively. Since most samples for determining chemical variables and colour had been taken from the surface water (depth 1 metre), only the surface data were used in the analyses. As normal distributions for the variables could not be achieved by means of log-transformation (Kolmogorov-Smirnov test for normality before and after transformation), a Kruskal-Wallis ANOVA for ranks or the Mann-Whitney Rank Sum test were used to test the untransformed data. Multiple comparisons, if needed, were performed using the formula:

$$\left| \bar{R}_i - \bar{R}_j \right| > z^*_{\alpha/[k(k-1)]} \sqrt{\frac{N(N+1)}{12}\left(\frac{1}{n_i}+\frac{1}{n_j}\right)}, \quad (1)$$

where $\bar{R}$ is a mean of ranks, z^* is a point from the table of normal distribution (2.39 in all cases in these analyses), the level of α is 0.05 and k is the number of groups. All the statistical calculations except for the multiple comparisons, which were calculated by hand according to Eq. 1, were performed with SPSS, ver. 13.0, for Windows.

Results

Chemical and physical features

Only minor differences in chemical parameters were found between water samples from different stations and depths in 2005 (Table 1). The water was brown (about 70–100 mg l⁻¹ Pt) and transparency values varied from 1.5 to 2.0 metres. Moderately low phosphorus (mean 12–13 μg l⁻¹)

Table 1. Water quality parameters (mean; range) at a depth of 1 metre in Lake Pyhäselkä at three sampling stations in May–June and August 2005 ($n = 6$).

| Sampling station	Kokonluoto	Pyhäsaari	Noljakka
Temperature (°C)	13.1; 8.8–17.0	13.4; 9.1–17.2	13.9; 9.2–17.2
Secchi depth m	1.9; 1.6–2.0	1.8; 1.5–1.9	1.7; 1.5–2.0
Turbidity FNU	1.3; 0.9–1.7	1.4; 1.0–1.9	1.7; 1.1–2.2
Colour (mg l⁻¹ Pt)	75; 70–80	77; 70–80	83; 70–100
P_{tot} (μg l⁻¹)	12; 10–17	12; 9–14	13; 11–15
PO_4-P (μg l⁻¹)	5; 4–8	5; 4–7	4; 3–6
NO_3-N (μg l⁻¹)	135; 112–163	123; 99–145	114; 105–136
N_{tot} (μg l⁻¹)	458; 401–491	454; 420–487	432; 413–474
Chlorophyll *a* (μg l⁻¹)	4.1; 3.3–4.9	3.9; 2.6–5.4	4.2; 2.4–6.4
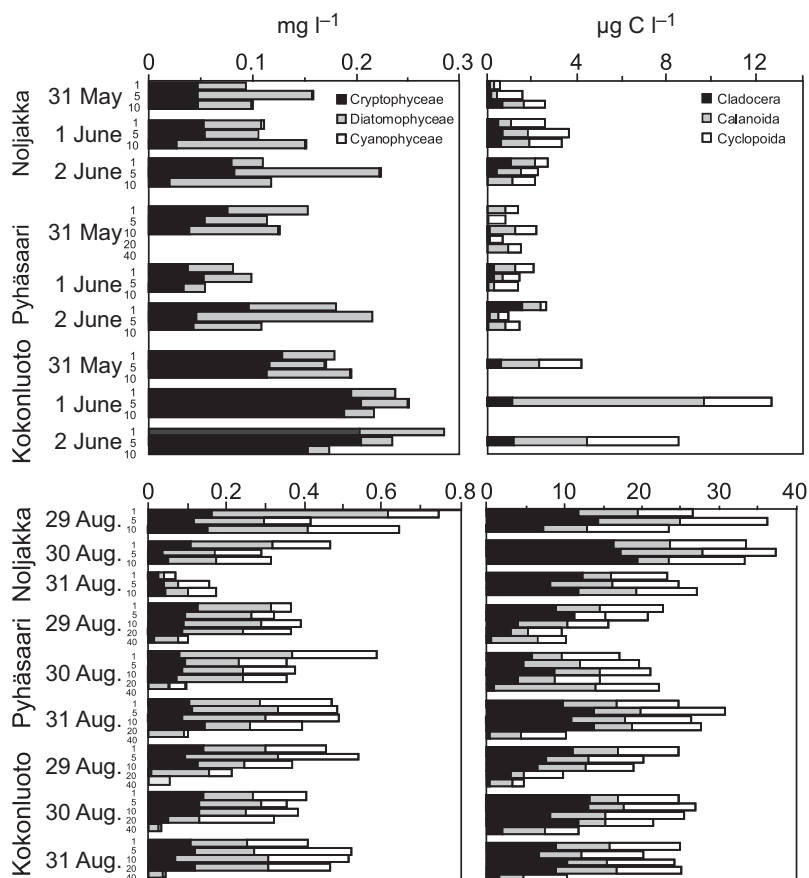
Fig. 3. Seasonal and short-time day-to-day variation in phytoplankton (mg l⁻¹) and zooplankton (µg l⁻¹) biomass in different water layers at three sampling stations in Lake Pyhäselkä in 2005. Phytoplankton samples in May–June were taken only from the depths of 1, 5 and 10 meters.

and chlorophyll *a* (mean 3.9–4.2 μg l⁻¹) values were characteristic of this lake.

During the first sampling period (31 May–2 June) the water mass behaved in different ways in different parts of the lake. The surface water was coldest in the eastern and southern parts, in the range 8.5–11.5 °C, and warmest in the western part, range 12.0–14.4 °C. Water temperatures in the same area varied by several degrees between successive days (Fig. 2). In August the surface water temperature was near the same on successive days and at all three stations. There was no stratification in the shallow northern area (Noljakka), but in the central basin (Pyhäsaari, Kokonluoto) there was a clear stratification and the depth of the epilimnion on consecutive days at the same stations varied between 20 and 35 m and temperatures in the metalimnion by several degrees (Fig. 2). Daily changes in the depth of the metalimnion were

used as a proxy for internal seiches and water currents, and was pronounced at the Pyhäsaari and Kokonluoto sampling stations throughout the period studied. Variation in the depth of metalimnion was highest at Kokonluoto in August. Water stability in Lake Pyhäselkä was with some exceptions always high (stability > 0). The theoretical period of oscillation for internal seiches in Pyhäselkä was around 4 hours.

Phytoplankton

The total phytoplankton biomass at the depths of 1, 5 and 10 metres in the epilimnion at the Noljakka, Pyhäsaari and Kokonluoto sampling stations in 2005 (Fig. 3) varied from 0.07 to 0.75 mg l⁻¹ (mean 0.28 mg l⁻¹), while the concurrent chlorophyll *a* content at a depth of 1 metre fluctuated between 2.4 and 6.7 μg l⁻¹ (mean
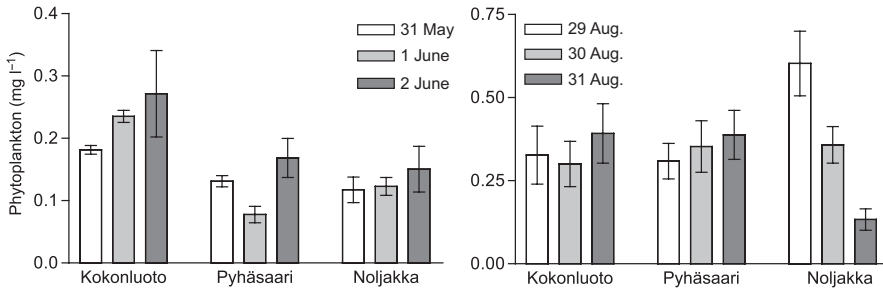
Fig. 4. Phytoplankton biomass (mean ± S.E.) in Lake Pyhäselkä at three sampling stations in June and August (pooled results for all depths). Biomasses differed statistically between consecutive sampling days only in August at one sampling station (Noljakka, *p* = 0.039). Plankton biomasses cannot be compared between sampling stations in the figure, as the numbers of depth layers are different.

4.5 μg l^{-1}). Total biomass was highest at the end of the summer, in August, at all three stations. The coefficients of variation (CV) between the ten replicates were 5.4% for the chlorophyll *a* results and 10% for the total phytoplankton counts. According to the Pearsson coefficients for the correlations between the fluorometer values and phytoplankton abundance were statistically significant ($p < 0.001$).

Horizontal and vertical differences were found in both phytoplankton biomass and species composition (Figs. 3 and 4). The biomass was concentrated in the epilimnion (1–10 metres), and figures were highest in May–June at Kokonluoto in the deep pelagial area and in August at the shallow Noljakka station. The amount of Cryptophyceae in the surface water (depths of 0–5 metres) was seen to have increased at the shallow sampling station of Noljakka on the last day of the spring expedition, while the amount of the diatoms was high at 5 metres. A similar increase was found in all water layers between 0 and 10 metres on the second and third days at the Kokonluoto sampling station in the pelagial area.

Day-to-day variation in phytoplankton biomass and species composition was found during all the expeditions and at all the sampling stations (Fig. 3). The biomass was highest on the last day at all the stations in spring. At this time biomass also halved during the second day at Pyhäsaari because diatoms decreased. During the last day in August the phytoplankton biomass at all depths at Noljakka dropped to one third of the measurements on the first day. Such a rapid change in daily biomass indicates major altera-

tions in the hydrological environment. A significant difference in biomass (pooled results for all depths) was noted on consecutive days only between first (29 August) and third (31 August) sampling days in August at Noljakka (multiple comparison, $p < 0.05$) (Fig. 4).

Zooplankton

The zooplankton biomass in June was highest at Kokonluoto, where the total crustacean biomass varied in the range 4.5–12.9 μg C l^{-1} (Figs. 3 and 5). The biomass at the depth of 5 m at Kokonluoto was more than three times that at either Noljakka or Pyhäsaari. Copepoda (mainly *Cyclops* spp. and *Limnocalanus macrurus*) predominated at all stations and depths in early summer. *Bosmina longispina* Leydig was the only cladoceran to account for over 5% of the crustacean biomass. At Pyhäsaari, *Cyclops* spp. and *Limnocalanus macrurus* were the dominant species, with the Cladocera (*Bosmina* spp., *Holopedium gibberum*, *Daphnia cristata* and *Leptodora kindti*) becoming more common on the second day, even though the temperature was lowest at that time. The proportion of *Bosmina longispina* increased drastically (from 6% to 41% at the depth of 1 m on the last day, 2 June). At Noljakka, the proportion of cladocerans (*B. longispina*, *Holopedium gibberum* and in some cases also *D. cristata*) was somewhat higher than at the other sampling stations, but *Cyclops* spp. and *Limnocalanus macrurus* were still the commonest species, as at the other stations.
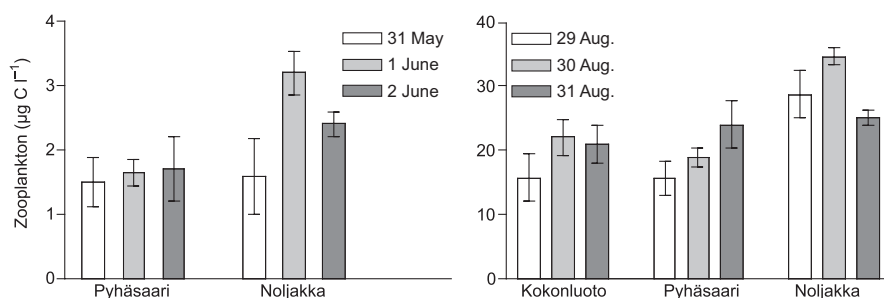
Fig. 5. Zooplankton biomass (mean ± S.E.) in Lake Pyhäselkä at three sampling stations in June and August (pooled results for all depths). The biomasses did not differ statistically between consecutive sampling days at any sampling station. Plankton biomasses cannot be compared between sampling stations in the figure, as the numbers of depth layers are different.

The biomass of crustacean zooplankton in August was seven-fold relative to the values recorded in June (Fig. 3). The biomass of small Cyclopoida (*Mesocyclops leuckarti* and *Thermocyclops oithonoides*) in the surface layers was high at this time at all stations, while the dominant species at the depth of 40 metres were *Limnocalanus macrurus* and *Cyclops* spp. Apart from some small Cyclopoida, *B. longispina*, and *D. cristata*, were common at Kokonluoto, except on the last day, when cladocerans were almost absent. *Bosmina longispina* was not as common at Pyhäsaari as it was at Kokonluoto. The biomass at Noljakka was higher than that at Kokonluoto and Pyhäsaari in August, with the small cyclopoids (*Mesocyclops leuckarti* and *Thermocyclops oithonoides*) and *Daphnia cristata* dominating the assemblage.

Because of the high variation, the biomasses (all depths pooled) did not differ statistically

between consecutive sampling days at any of the stations (Fig. 5). The total zooplankton biomass in the hypolimnion (40 m) had increased on 30 August relative to the previous day, 29 August, and had fell again by the following day, 31 August.

Pelagic plankton communities and environmental variables

The most obvious differences in phytoplankton and zooplankton abundances and biomass in Lake Pyhäselkä were seasonal ones (June *vs.* August), and these were statistically highly significant (Mann-Whitney Rank Sum test: *p* < 0.0005) (Table 2). The water quality parameters, including nutrients (phosphorus, nitrogen), colour and temperature, also differed significantly between the months (Mann-Whitney

Table 2. Influence of sampling time, place and depth on certain biological, chemical and physical variables in Lake Pyhäselkä in June and August 2005. The statistical analysis is based on samples taken from three stations and three water depths (1, 5 and 10 metres) at each station. Samples for determining phosphorus, nitrogen and colour were taken from the surface water (depth 1 m). Non-parametric Kruskal-Wallis ANOVA (daily, station, depth) for ranks or the Mann-Whitney Rank Sum test (months) was used.

	Dependent variable					
Independent variable	Phytoplankton	Zooplankton	Temperature	P_{tot}	N_{tot}	Colour
Day (31 May, 1 June, 2 June)	$P = 0.277$	$P = 0.428$	$P = 0.797$	$P = 0.164$	$P = 0.670$	$P = 0.565$
Day (29 Aug., 30 Aug., 31 Aug.)	$P = 0.426$	$P = 0.299$	$\boldsymbol{P < 0.0005}$	$P = 0.721$	$P = 0.151$	$P = 0.565$
Month (June *vs.* August)	$\boldsymbol{P < 0.0005}$	$\boldsymbol{P < 0.0005}$	$\boldsymbol{P < 0.0005}$	$\boldsymbol{P < 0.0005}$	$\boldsymbol{P < 0.0005}$	$\boldsymbol{P = 0.001}$
Place in June	$\boldsymbol{P = 0.002}$	$\boldsymbol{P = 0.005}$	$P = 0.650$	$P = 0.549$	$P = 0.288$	$P = 0.102$
Place in August	$P = 0.428$	$\boldsymbol{P = 0.023}$	$P = 0.083$	$P = 0.134$	$P = 0.315$	$P = 0.565$
Depth (1, 5, 10 m) in June	$P = 0.546$	$P = 0.730$	$\boldsymbol{P < 0.0005}$	–	–	–
Depth (1, 5, 10 m) in August	$P = 0.576$	$P = 0.889$	$P = 0.867$	–	–	–

Rank Sum test: $p = 0.001$ for colour and $p < 0.0005$ for the other variables). Short-interval day-to-day variation was obvious for most variables in both sampling periods, but statistically significant only in the case of temperature in August (Kruskal-Wallis ANOVA for ranks: $p < 0.0005$), since the mean temperature was significantly lower on the third sampling day (31 August) than on the previous two days (multiple comparison: $p < 0.05$).

The influence of sampling station on the phytoplankton and zooplankton biomass was statistically significant in June (Kruskal-Wallis ANOVA for ranks: $p = 0.002$ and $p = 0.005$, respectively), but this was true only for zooplankton (Kruskal-Wallis ANOVA for ranks: $p = 0.023$) in August (Table 2). The phytoplankton biomass at Kokonluoto was higher than at either Pyhäsaari or Noljakka in June (multiple comparison: $p < 0.05$), and the biomass of zooplankton in the same month was also higher at Kokonluoto than at Pyhäsaari (multiple comparison: $p < 0.05$) but not significantly higher than at Noljakka. The biomass of zooplankton in August was higher at Noljakka than at Pyhäsaari (multiple comparison: $p < 0.05$), but the biomass at Kokonluoto did not differ significantly from those at Noljakka and Pyhäsaari. The influence of sampling depth was statistically significant only with regard to temperature in June (Kruskal-Wallis ANOVA for ranks: $p < 0.005$), when the water temperature was higher at the depths of 1 and 5 metres than at 10 metres (multiple comparison: $p < 0.05$). The correlation between phytoplankton and zooplankton abundances was high ($r^2 = 0.50$, $n = 60$), even if not in biomass, indicating obvious association between these variables.

Discussion and conclusions

The results show that the seasonal and short-interval variation in plankton abundance is high and that these patterns are highly dynamic and can change, and that the association between the physical, chemical and biological environment can be quite complex. Large-scale patterns in the distribution of plankton may be generated by a variety of vectorial and stochastic-vectorial processes such as currents and upwelling events and by physicochemical alterations (Pinel-Alloul *et al.* 1999). It has been suggested that the combined action of wind-induced water movements and the behaviour of organisms can result in large-scale spatial heterogeneity (Pinel-Alloul 1995, Thackeray *et al.* 2004).

The occurrence of horizontal temperature variations and changes in the depth of the metalimnion on successive dates confirmed that a large-scale, non-random process was responsible for generating the physical structure of the pelagic zone in Lake Pyhäselkä. The rapid changes in daily plankton biomasses in Lake Pyhäselkä were assumed to indicate major alterations in the hydrological environment. The period of oscillation of internal seiches in Lake Pyhäselkä is approximately 4 hours, but internal seiches cannot explain the variations observed in the temperature profiles, because the temperature measurements were made almost 24 hours apart. Wind-induced water movement explained almost half of the spatial variation in Lake Windermere, and the large-scale spatial variability in zooplankton abundance matched that in the physical environment (Thackeray *et al.* 2004). It was also shown there that the nature of the spatial pattern and that of the association between the physical environment and zooplankton heterogeneity varied over time. In Lake Pyhäselkä, the highest phytoplankton and zooplankton biomass were in May–June in the deep central basin (Kokonluoto), but in August in the shallow northern area (Noljakka) (Fig. 3). The thickness of the epilimnion varied and the biomass of zooplankton increased in the metalimnion (20 m) at the deep stations (Kokonluoto and Pyhäsaari) on successive days. Rinke *et al.* (2007) found a positive correlation between zooplankton abundance and water temperature, and a significant dependency on successive dates. Temperature and climate are thought to be the proximate factors controlling zooplankton abundances in large lakes during spring and summer (Patalas 1969, Patalas and Salki 1992, Stockwell and Sprules 1995, Pinel-Alloul *et al.* 1999), and the direct influence of water temperature could have operated through the temperature-dependent metabolism and development of zooplankton. The differences in the responses of crustaceans to temperature may be due to the different thermal requirements of the taxa.

Fine-scale horizontal variability in zooplankton distribution has often detected in response to the presence and feeding of planktivorous fish (Pinel-Alloul 1995, Jeppesen *et al*. 1997, Romare *et al*. 2003). In the oligotrophic Lake Stechlin (Mehner *et al*. 2005) the distributions of fish, zooplankton and phytoplankton correlated with water temperature and nutrient concentration, and water temperature has been found elsewhere to influence the timing and magnitude of diel vertical migrations in zooplankton (Winder *et al*. 2003) and fish (Viljanen 1983, Hamrin and Persson 1986). Thus any valid description of the composition of the trophic variables in a deep lake has to consider the interplay between diurnal-nocturnal and temperature-dependent vertical distribution patterns in the populations (Mehner *et al*. 2005).

Even though there was no clear trophic gradient in Lake Pyhäselkä, some horizontal differences in plankton abundance and community structure were observed. *Daphnia cristata* was more common in the northern part of Pyhäselkä in August 2005 and *Bosmina longispina* in the deep central and southern parts of the lake. In 1992, when the species composition of the whole of Lake Pyhäselkä was studied, *Daphnia* and *Eudiaptomus* were dominant in southern pelagial zone, while *Bosmina* was more typical of the western part of the lake (Karjalainen *et al*. 1996a).

The abundance of phytoplankton and zooplankton in the northern part of the lake (Noljakka) in August 2005 decreased on the third day relative to the previous days, probably due to the change in wind and current direction and the drop in temperature, while neither the temperature difference nor the change in abundance was so evident in the deep southern part of the lake. Zooplankton was distributed fairly evenly between the water layers down to the depth of 20 m, and decreased at 40 m (Fig. 3). Some daily variation was observed, however, especially at greater depths. This was assumed to be due to wind-induced metalimnion oscillation in the deep central basins, which affected the level of the metalimnion and altered the temperature at the same water depth by more than five degrees on successive days (Fig. 2). In Bautzen Reservoir, the vertical distribution was strongly affected by downwelling and internal waves (Rinke *et al*. 2007). Downwelling enlarged the thickness of the epilimnetic layer and, hence, led to high zooplankton abundances down to relatively deep water strata indicating lateral transport of zooplankton. As water stability in Lake Pyhäselkä was usually high (stability > 0), this may have kept the phytoplankton in the warm, better illuminated upper water layers by reducing vertical mixing and enhancing phytoplankton growth. The positive correlation between the abundances of phytoplankton and zooplankton indicated an obvious association between these variables.

Our results have implications for monitoring of lake plankton communities. Large fluctuations of plankton biomass can be set up by internal waves or by wind-driven horizontal transport if the lake is exposed to strong winds (Rinke *et al*. 2007). Sampling sites are especially susceptible to these hydrodynamically caused fluctuations. Such effects may become even stronger in large lakes, like Pyhäselkä, where internal waves are affected by the Coriolis force. Monitoring programmes in lakes should therefore use information about hydrophysical environment, in order to account for possible effects of internal waves or wind-driven lateral transport processes on the distribution of plankton organism (Rinke *et al*. 2007).

Our measurements have produced a dataset that can be used in the calibration and validation of a 3D model application for Lake Pyhäselkä. This model can then be used to truly study the mechanisms that lead to the spatial heterogeneity of the plankton.

We can conclude from our results that (1) phytoplankton and zooplankton exhibit seasonally and spatially heterogeneous distributions which may be related to the hydrodynamic properties of the water body; (2) the most obvious differences in phytoplankton and zooplankton abundances and biomass, and in the water quality parameters, were seasonal ones, and these were statistically highly significant ($p < 0.0005$); (3) there were obvious small-scale, short-interval day-to-day variations in temperature and the horizontal and vertical distribution of phytoplankton and zooplankton; and (4) the validity of a comparative inter-lake approach and long term monitoring of one lake would greatly depend on

the question of whether the samples had been taken in the same month, at the same place and at comparable points in the vertical water column.

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