



Steady state phytoplankton in a deep pre-alpine lake: species and pigments of epilimnetic *versus* metalimnetic assemblages

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Abstract

The vertical distribution pattern of algal species, chlorophylls and specific carotenoids present in the dimictic pre-alpine Ammersee (Bavaria, Germany) are given for the year 2001. A detailed taxonomic list of the phytoplankton species is recorded, along with light micrographs and detailed descriptions of the flagellates. A deep chlorophyll maximum, mainly built by *Planktothrix rubescens*, was common in this deep mesotrophic lake. The three most dominant species among 83 identified taxa alternated seasonally and reached significant biovolumes in both the epilimnion and the metalimnion (*Planktothrix rubescens* > *Ceratium hirundinella* > unicellular centric diatoms > *Asterionella formosa* > *Fragilaria* spp. > *Anabaena lemmermannii* > *Phacotus lenticularis* and less frequent dominant was *Rhodomonas minuta*). We define a steady state phytoplankton assemblage in Ammersee as a stable community in terms of species composition and standing crop. The stability of species composition was measured by Bray-Curtis similarity between monthly samples and indicate the change of individual biovolumes of species from month to month. The stability of standing crop was evaluated by the net change of total biovolume for the same time intervals. Focussing on steady state phytoplankton assemblages we compared three spatially heterogeneous environments for vertical niche separation within the top 12 m: the euphotic epilimnion (2 and 5 m), the euphotic metalimnion (7 m) and the metalimnion below the euphotic zone with dim-light less than 1% (10 and 12 m). The definition of a steady state assemblage on both ends hold true only for metalimnetic layers at dim-light levels below 1% in Ammersee. At this metalimnetic layer more than 80% similarity in phytoplankton composition between successive monthly samples was reached, associated with almost zero net changes of total biovolume only. The greater the contribution of the three most dominant taxa to biovolume, the higher were the Bray-Curtis similarities at metalimnetic depths below the euphotic zone. Zooplankton biomass had very little effect on species assemblages in the metalimnion, while parameters related to stratification (Schmidt stability) as well as those of trophic (TP, Chl) correlated with species changes. The similarity values between successive monthly samples from all the euphotic layers never reached more than 60% and were usually significantly lower, even if biovolume net changes were around zero. Both the high fluctuations of the ratio of photosynthetic *versus* photo-protective carotenoids (PSC:PPC) and the statistical significance of correlations between the change of species and environmental-biotic parameters separate the euphotic layer of the top 7 m as a homogenous community from deeper strata. At all sampling depths within this euphotic zone the increase of sunshine duration was associated with an increase of the carotenoid ratio PSC:PPC, but no relationship was found for the deeper layers. The change of species in the euphotic layer was not significantly related to thermal stability, TP or the dominance structure of phytoplankton, but linked with the zooplankton biomass and therefore seemed to be top-down controlled. From our observations, we can conclude that only during stratification and only in the metalimnion below the euphotic zone steady state assemblages can be expected in the deep mesotrophic Ammersee.

Introduction

The thermodynamic term 'steady state' originally coined by studies on chemical reaction kinetics is also used to define growth in continuous culture systems, to describe the persistence of biota, and relatively stable conditions as a whole in an ecosystem like the rain forest or parts of the ocean (e.g. Bannister, 1974; Janasch, 1974; Sommer, 1985). Here we define a steady state phytoplankton assemblage as a stable community in terms of species composition and standing crop.

Steady state assemblages in the microbiological sense could exist only if production and losses were perfectly balanced independent of time. Intermediate disturbance hypothesis and resource ratio hypothesis focus on the dynamic of abiotic factors, mainly nutrients, and emphasise the bottom up control on the structure of algal community (e.g. Tilman et al., 1982; Reynolds et al., 1993). Species diversity shaped by nutrients is seen as the response to the number of limiting nutrients (e.g. Interlandi & Kilham, 2001) and to the dynamic of nutrients defined by both quantities – the magnitude and the frequency of pulses (e.g. Sommer, 1995; Polishchuk, 1999). The top-down control on diversity is complex as well as reviewed in Hixon (2002). Approach on chaos theory stresses that the feedback in plankton system itself generates internal dynamics preventing the system from coming to equilibrium (Scheffer et al., 2003).

Results from multispecies chemostat experiments by Sommer (1983) suggest that an inoculum-independent equilibrium in phytoplankton would need at least 3–6 weeks of constant environmental conditions in a lake. We can not expect such a continuous culture situation of constant environmental conditions in nature because of (i) a great variety of factors which may have an influence on phytoplankton succession, and (ii) the seasonality in temperate lakes. Steady state conditions may, however, at least be found in stratified lakes developing simultaneous spatially separated phytoplankton associations in different strata (Haffner & McNeely, 1989; Reynolds, 1992; Lindholm, 1992). We expect that most of the abiotic factors which could have a major influence on phytoplankton dynamics are strongly fluctuating in the surface layer, favouring higher dynamics in species change in the surface than in metalimnetic layers. We performed this study on a mesotrophic, dimictic alpine lake with a deep chlorophyll maximum, mainly built by *Planktothrix rubescens*. During summer stratification from 1997 to 2001, the metalimnetic phytoplankton below the

euphotic zone reached biovolumes on average 30% higher than those in the epilimnion (Teubner, unpubl.). The main emphasis in this paper is on the vertical distribution pattern of algal species and their specific pigments. For practical purposes three criteria must be met according to Sommer et al. (1993) to consider an algal community to be in steady state: (i) no more than three species contribute more than 80% to the total biomass, (ii) the persistence of these species for more than 1–2 weeks and (iii) during this period the total biomass does not significantly change. In this phytoplankton study in Ammersee, we searched for such time periods and depth layers in which steady states are most likely.

We hypothesise that significant differences between the epilimnetic and metalimnetic phytoplankton become evident by both (i) the composition and (ii) the change of composition. In particular, we used a measure for the similarity between successive phytoplankton samples in the respective depth layers to evaluate the monthly change of species composition at different depth layers. We evaluate the applicability of the definition of steady state assemblages given above.

Method

Site description

Ammersee is a mesotrophic dimictic pre-alpine lake near Munich (Bavaria in Germany) with a maximum depth of 81 m and a water volume of $1750 \cdot 10^6 \text{ m}^3$. Further details on morphometry and trophy were described in Morscheid & Mayr (2002).

Sampling and data treatment

Monthly samples were taken between 10 and 11 a.m. at the deepest point in Ammersee from February to November 2001. Biovolume of phytoplankton of the depth samples 2, 5, 7, 12 and 15 m was estimated from microscopically counted abundance and size measurements of single units of cells or colonies. Samples for pigments and chemical parameters were taken from 0, 2, 5, 7, 10, 12, 15, 20 and 30 m. Pigments were analysed by high performance liquid chromatography (HPLC) in accordance with Wright et al. (1991). One litre of lake water was filtered (Whatman GF/F). The filter was frozen and extracted by 90% acetone. To maintain the calibration settings, a mixed pigment standard was used containing caroten-

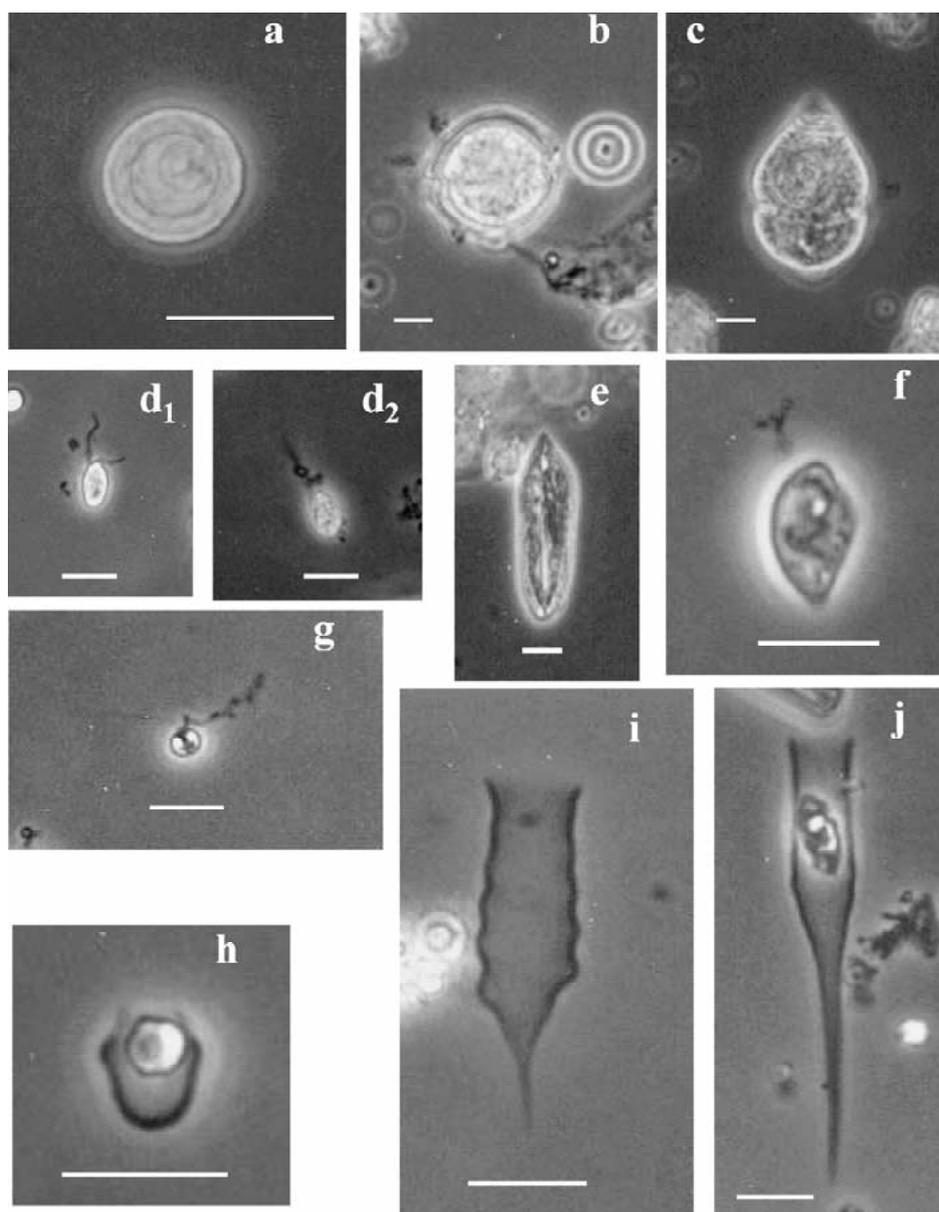


Plate 1. Flagellates from Ammersee. (A) *Phacotus lenticularis* (B) *Peridiniopsis* spec. (C) *Gymnodinium helveticum*, (D 1–2) *Katablepharis* cf. *ovalis*, (E) *Cryptomonas* cf. *erosa*, (F) *Rhodomonas lens*, (G) *Chrysochromulina parva*, (H) *Kephyrion* cf. *rubri-claustri*, (I) *Dinobryon acuminatum*, (J) *Dinobryon bavaricum* (bars = 10 μ m).

oids in quantitative proportion to chlorophyll-*a* as measured in algal cultures and described in Wilhelm et al. (1991), respectively. Carotenoids in Figure 4 were categorised according to their distinct function as ‘photo-synthetic carotenoids (PSC)’, such as fucoxanthin and fucoxanthin-like pigments, peridinin, prasinoxanthin and α -carotene involved in light harvesting, and photo-protective carotenoids (PPC), which

are the remaining carotenoids protecting the cells against photo-oxidation (Rowan, 1989; Bricaud et al., 1995; Stuart et al., 1998). The ratio PSC:PPC was related to the sunshine duration averaged over the 21 days before sampling, because this time interval was best related to the pigment ratio when compared with stepwise intervals from 1 to 33 days.

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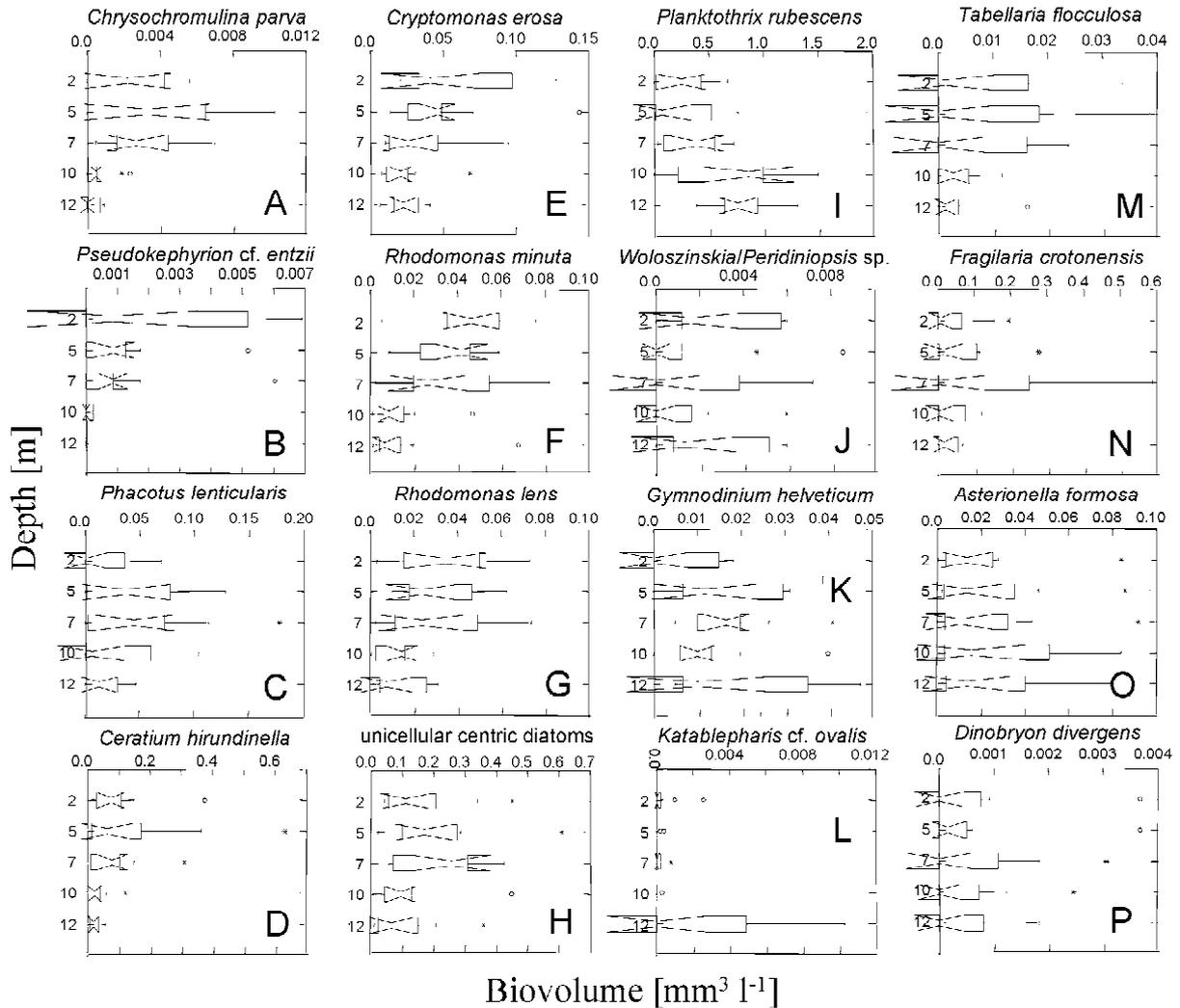


Figure 2. Vertical distribution of the biovolume in $\text{mm}^3 \text{l}^{-1}$ of haptophytes (A – *Chrysochromulina parva*) chrysophytes (B – *Pseudokephyrion cf. entzii*), chlorophytes (C – *Phacotus lenticularis*), dinoflagellates (D – *Ceratium hirundinella*, J – *Woloszinska/Peridiniopsis*, K – *Gymnodinium helveticum*), cryptophytes (E – *Cryptomonas erosa*, F – *Rhodomonas minuta*, G – *R. lens*, L – *Katablepharis cf. ovalis*), diatoms (H – unicellular centric diatoms, M – *Tabellaria flocculosa*, N – *Fragilaria crotonensis*, O – *Asterionella formosa*) and cyanobacteria (J – *Planktothrix rubescens*). Notched box-whisker plots as in Figure 1.

more evenly distributed in the water column. Significant differences in the vertical distribution of individual species are indicated by non-overlapping notches in the box-plots of Figure 2. In particular, *Ceratium hirundinella*, *Cryptomonas erosa* and *Rhodomonas minuta* had significant higher biovolumes at 2 or 5 m, and *Chrysochromulina parva* at 7 m when compared with deep layers. In contrast, *Planktothrix rubescens* developed significant higher biovolumes only at 12 m.

The general vertical distribution pattern for the different algal groups is shown by their respective

pigments in Figure 3. Both chlorophyll-*a* and β -carotene, which are ubiquitous or virtually present in all algae showed the same vertical distribution with a maximum at 10 m indicating the highest phytoplankton biovolume in the deep layer (Fig. 3A, D). Both were significantly related to total biovolume of phytoplankton (chlorophyll-*a*, $r = 0.86$; β -carotene: $r = 0.65$, $n = 70$). Major and minor carotenoids for cyanobacteria shown in Figure 3 E–H and echinenone (not shown) had the similar vertical pattern as chlorophyll-*a* and β -carotene. The close relationship

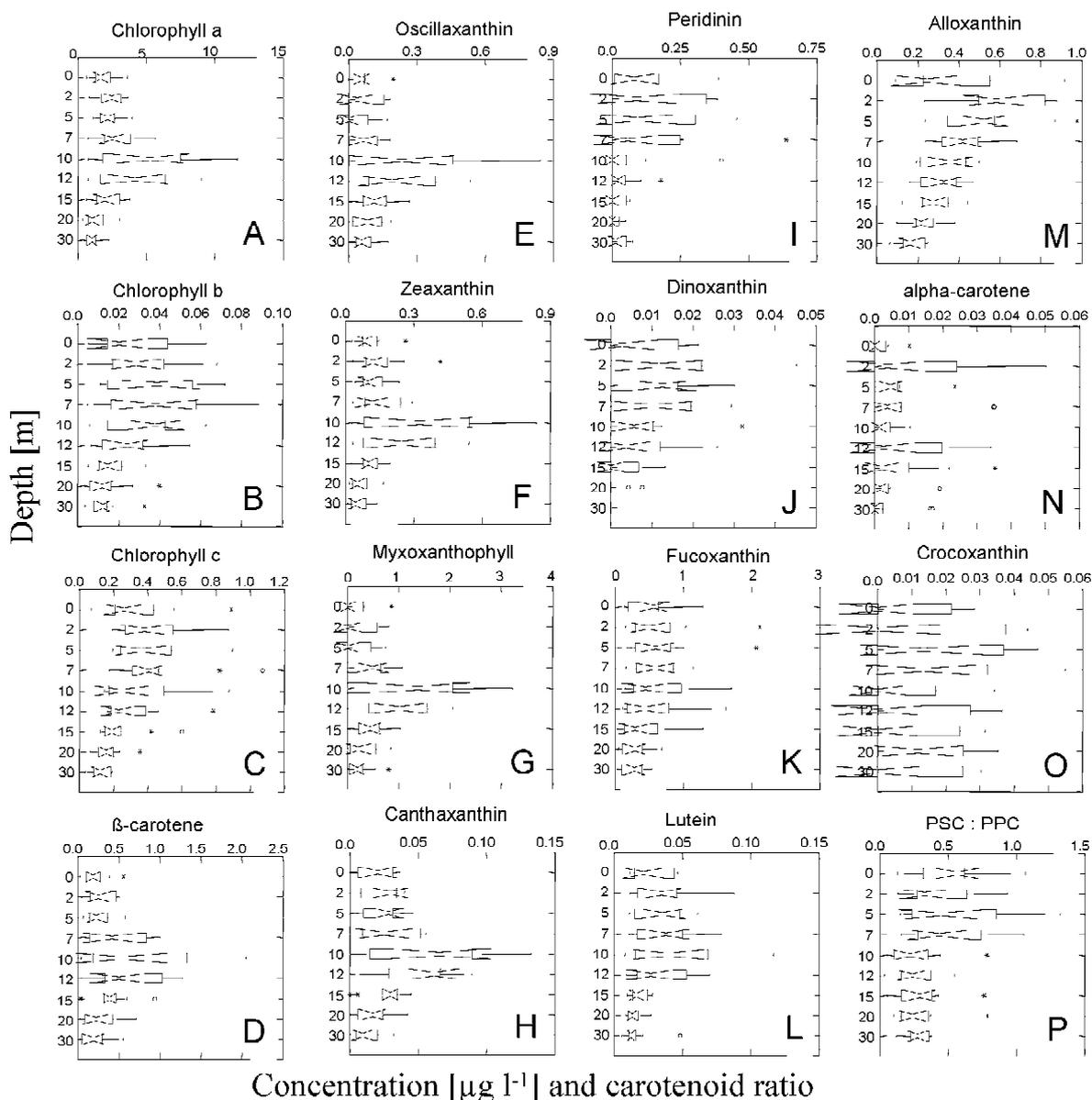


Figure 3. Vertical distribution of the concentration of pigments in $\mu\text{g l}^{-1}$ (A–C chlorophylls, D–O carotenoids) and the carotenoid ratio PSC:PPC (P, photo-synthetic carotenoids: photo-protective carotenoids).

between these pigments and both the total biovolume of the cyanobacteria and of *Planktothrix rubescens* indicates the dominance of this single species among the photoautotrophic prokaryotes (oscillaxanthin: $r = 0.80$ and 0.81 , zeaxanthin: $r = 0.87$ and 0.87 , myxoxanthophyll: $r = 0.79$ and 0.80 , canthaxanthin: $r = 0.79$ and 0.79 , echinenone: $r = 0.88$ and 0.88). Peridinin and dinoxanthin, characteristic pigments in photosynthetic dinoflagellates, correlate with the total

biovolume of dinoflagellates as well as with that of *Ceratium hirundinella* (Fig. 2D and 3I–J; peridinin: $r = 0.65$ and 0.64 ; dinoxanthin $r = 0.37$ and 0.33 , respectively). The predominantly epilimnetic occurrence of *Ceratium hirundinella* was highlighted by both the biovolume of this species and the total amount of the respective carotenoids. The major carotenoid alloxanthin in cryptophytes was closely related to the biovolume of this algal group, the sum of *Cryptomo-*

nas species and, in particular, to *C. erosa* ($r = 0.68$, 0.69 and 0.73 , respectively), while crocoxanthin was correlated to all *Rhodomonas* species but especially to *R. lens* ($r = 0.54$ and 0.58 , respectively). The epilimnetic dominance of the cryptophytes in general is illustrated by alloxanthin, while a more even distribution from the surface down to the deepest layers was emphasised by crocoxanthin. The major pigments of the chlorophytes and of the amalgamated group of diatoms and chrysophytes were closely related to the respective algae (lutein: $r = 0.65$, fucoxanthin: $r = 0.84$). Both pigments are again examples for evenly distributed pigments in the vertical 0–12 m.

Vertical pattern of the ratio of photo-synthetic versus photo-protective carotenoids

The ratio of lipophilic accessory photo-synthetic versus photo-protective carotenoids (PSC:PPC) was higher and more fluctuating in the surface layer 0–7 m than at deeper depth (Fig. 3 P). Different behaviour of phytoplankton in the two layers was indicated by the relationship between this carotenoid ratio and the sunshine duration throughout the year (Fig. 4). At all sampling depths within the euphotic zone (≤ 7 m, Fig. 5 B) the phytoplankton was related to increased sunshine duration by the relative increase of photo-synthetic versus photo-protective carotenoids (Fig. 4 A), but no relationship was found for the deeper layers (Fig. 4 B). The greatest response to sunshine duration was found at 5 m as indicated by a higher slope when compared with other surface layers. The mean relative light intensities in the euphotic zone at 2 m, 5 m and 7 m were 33%, 6.5% and 2.3%, respectively, in the metalimnion below the euphotic depth at 10 m and 12 m still 0.51% and 0.19%.

Seasonal dynamics of phytoplankton and controlling factors

The seasonal dynamics of chlorophyll-*a* concentration, the stability of stratification in the water column (Schmidt stability), the depth of the euphotic zone (z_{eu}) and the mixing layer (z_{mix}) are shown in Figure 5. During thermal stratification the euphotic layer was deeper than the mixing depth. The sampling depths 2 and 5 m were representative for the epilimnetic layer during thermal stratification. Samples from 7 m represent the bottom layer of the euphotic zone and were already in the metalimnion. 10 and 12 m were always the dim-light layers below the euphotic zone

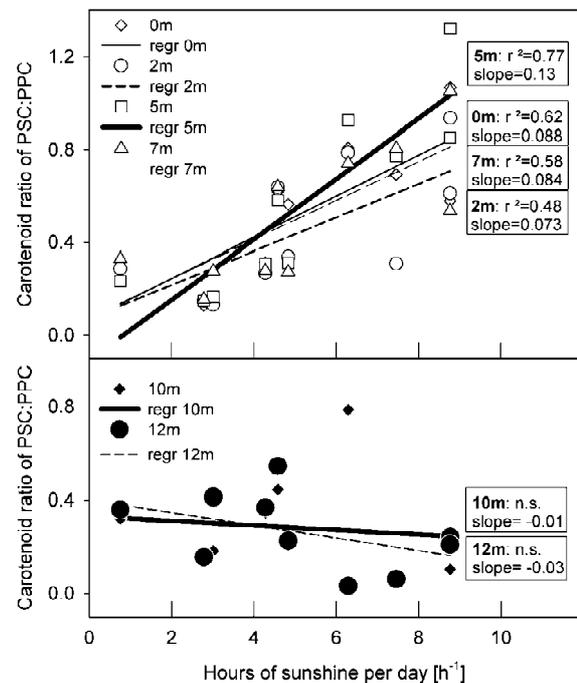


Figure 4. The hours of sunshine per day versus the carotenoid ratio PSC:PPC as in Figure 3 P for epilimnetic (A) and metalimnetic layers (B).

in the metalimnion. With the onset of stratification the chlorophyll concentration in the metalimnion became much higher than in the epilimnion (Fig. 5 A). From May to September, the three most dominant species reached on average 77–75% of total biovolume at 2 and 5 m respectively, 82% and 88% at 10 and 12 m. Most of these taxa were dominant in both the epi- and the metalimnion (*Planktothrix rubescens* > *Ceratium hirundinella* > unicellular centric diatoms > *Asterionella formosa* > *Fragilaria* spp. > *Anabaena lemmermannii* > *Phacotus lenticularis* and less frequent dominant was *Rhodomonas minuta*). In contrast, *Cryptomonas erosa* and *Gymnodinium helveticum* were dominant only in the epi- or the metalimnion respectively. In terms of the number of species, up to 9 taxa, on average 3–4 taxa contributed to at least 80% of total biovolume in the epilimnion, but only up to 6 taxa, on average 2–3 to that in the metalimnion.

The change of species in phytoplankton was evaluated by the similarity between two successive monthly samples (Bray-Curtis, see method). A low value was calculated between the samples February and March (2–3) for each depth (Fig. 5 A). Almost the same low value of similarity was calculated for the sampling

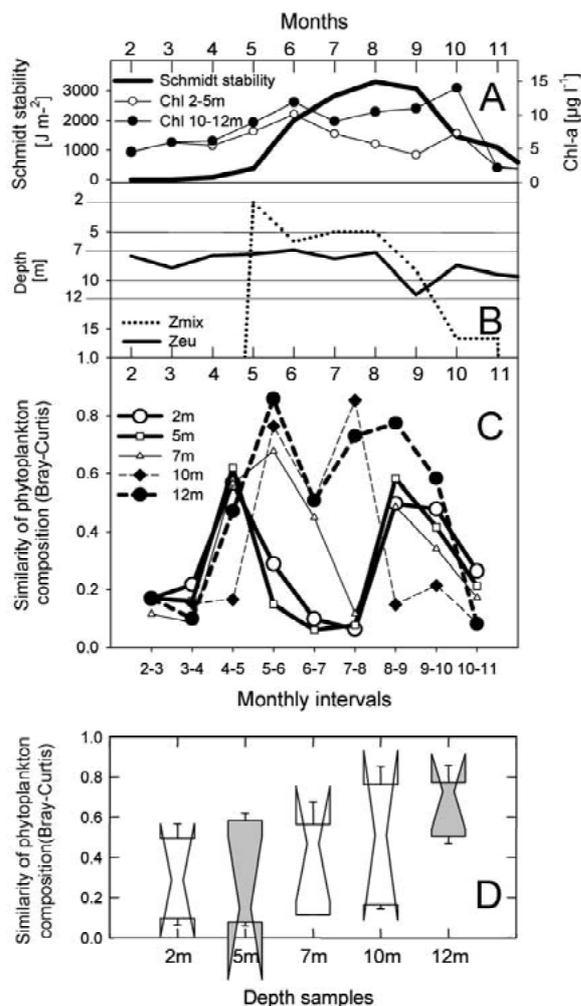


Figure 5. (A) Stability of stratification in the water column (Schmidt stability), concentration of chlorophyll-*a* in the upper epilimnion (2–5 m) and in the metalimnion (10–12 m). (B) Euphotic (z_{eu}) and mixing depth (z_{mix}). (C–D) Change of individual species biovolumes in phytoplankton as similarity by Bray-Curtis between successive monthly samples (C) and between layers during thermal stratification from May to September as box-whisker plot (D). Significant differences between depth layers 5 m and 12 m in D are indicated by non-overlapping confidence (see ‘Method’).

pair March–April (3–4) for all depths. In other words, the share of biovolume of individual species in March and April was quite different from that of the previous month. Significant higher similarity values were reached from April to May before the onset of stratification indicated by low values of Schmidt stability and the narrow mixing depth (Fig. 5 A–C). A further increase in the similarity at 7, 10 and 12 m was concomitant with the onset of thermal stratification between May and June. Particularly high similarities,

indicating a stable species composition, were measured for the phytoplankton at 12 m from May to September. The similarity at 10 m follows the same trend but dropped off between August and September. At the same time we measured a decrease of stability of the thermal stratification, a mixing down to about 11 m (z_{mix}) and an increase in euphotic depth (z_{eu}).

The opposite trend was observed for the epilimnetic layer. With the onset of stratification, the similarity decreased again (5–6). Stable phytoplankton species composition could not be observed at any time between May and August. With decreasing stability of the thermal stratification and deeper mixing between August and September the similarity of phytoplankton composition decreased even at 2 and 5 m.

The similarity of phytoplankton between October and November (10–11) was as low as between March and April (3–4). Therefore for both mixing periods, the same unstable phytoplankton composition was observed for all the investigated layers.

All similarity values for the stratified period May to September are compared in the box-plots of Figure 5D for all individual depths. High median values indicate the general trend of a stable phytoplankton composition in the metalimnion (7–12 m). At the same time, the epilimnetic phytoplankton changed significantly from month to month, as shown by low similarity values. In particular, a significant difference in the change of phytoplankton composition at 5 m and 12 m is shown by non-overlapping notches.

The correlation between Bray-Curtis similarity and different variables is given in Figure 6. At all sampling depths within the euphotic zone (≤ 7 m, Fig. 5 B) the Bray-Curtis similarity was significantly related only to the biovolume of zooplankton (rotifers and metazoan zooplankton). Bray-Curtis values for the metalimnetic zone below the euphotic zone, 10 and 12 m, were significantly related to all parameters except zooplankton. The close correlations to z_{eu}/z_{mix} and Schmidt stability (SCHMIDT) were in accordance with the general trend of low similarity values during mixing in spring and autumn, but high values during stratification in summer as shown in Figure 5. The higher the concentrations of chlorophyll-*a* and TP, the more similar was the phytoplankton composition between successive months, especially at 10 m. The more the biovolume amount contributed by the three most dominant taxa, the higher were the Bray-Curtis similarities at both metalimnetic depths below the euphotic zone.

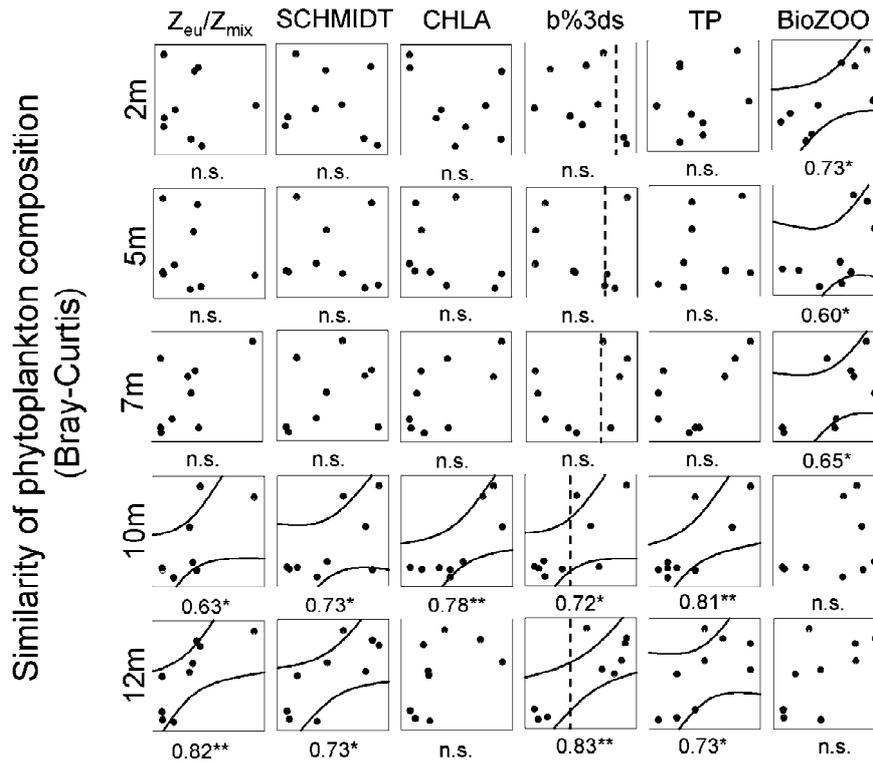


Figure 6. Pearson correlation between the similarity of phytoplankton between successive samples (Bray-Curtis) and variables: the ratio between euphotic to mixing zone (z_{eu}/z_{mix}), the stability of stratification in the water column (Schmidt stability, Schmidt), Chlorophyll-*a* concentration (Chl-*a*), the percentage contribution of the three most dominant species to phytoplankton biovolume at each sampling date (b%3ds, 80% marked dashed line), total phosphorus concentration (TP) and the biovolume of zooplankton (BioZoo). Except z_{eu}/z_{mix} and Schmidt stability the correlations were calculated between both values of the respective depths. Data cover all sampling intervals ($n = 9$, February–November). Coefficients and 0.95 confidence intervals of regression lines are shown only for significant correlations. Significance is marked as: *- $P < 0.05$, **- $P < 0.01$, n.s. - not significant.

Discussion

A metalimnetic deep chlorophyll maximum below the euphotic zone mainly built by *Planktothrix rubescens* as observed in Ammersee is common in deep meso-eutrophic lakes and can be assigned to one of the four main types of deep-living algal communities suggested by Adler et al. (2000). A number of species were common at deep layers in Ammersee even if less dominant than *Planktothrix rubescens*. This occurrence of species of various phytoplankton groups in the region of the deep chlorophyll maximum has also been described by other studies (e.g. Haffner & McNeely, 1989; Lindholm, 1992; Gervais, 1998; Flaim et al., 2003). The distribution of species ranging from the surface down to layers below the euphotic zone is discussed as temporary or stationary vertical niche separation, to avoid washing out and grazing, overcoming nutrient limitation by obtaining access to

enhanced or other nutrient reserves than at surface (e.g. Sommer, 1982; Jones, 1991, 1993; Arvola et al., 1991; Gervais, 1998). Oligotrophic alpine lakes, however, rarely have a deep chlorophyll maximum (e.g. Teubner, 2003).

Considering thermal stratification and light as relevant for vertical co-colonisation three spatially distinct environments for phytoplankton were allocated within the top 12 m in Ammersee: the euphotic epilimnion, the euphotic metalimnion and the metalimnion below the euphotic zone with dim-light less than 1%. The phytoplankton assemblages in these three spatial layers were confirmed by both the results of phytoplankton counting and the analysis of specific pigments (Schmid et al., 1998; Descy et al., 2000). Photosynthetic dinoflagellates as identified by peridinin, and particularly *Ceratium hirundinella*, were frequent in the euphotic epilimnion, which is in accordance with the hypothesis of vertical migra-

tion in dinoflagellates being mainly controlled by the underwater light (Heaney & Talling, 1980; Moore, 1981). *Chrysochromulina parva*, *Dinobryon divergens*, *Rhodomonas speciosa*, *Gymnodinium helveticum* and some diatoms were common in the epilimnion but had also pronounced biovolume peaks in the euphotic metalimnion. Most of them are flagellated species known for specific patterns of diel vertical migration in response to daily fluctuating conditions in the environment (e.g. Sommer, 1982; Rott, 1983; Sommer, 1988; Arvola, 1991; Gervais, 1997 a). Many species do not avoid migration even through steeper gradients near the metalimnion which all could support a highly diverse phytoplankton structure along deep verticals in principle. The carotenoid ratio PSC:PPC suggests however, that the euphotic layer (≤ 7 m) can be seen as a homogenous community of photosynthetic organisms functionally related to the duration of sunshine throughout the year. The carotenoid ratio of phytoplankton layers below the euphotic zone was not related to sunshine duration nor were other ratios of lipophilic pigments such as, e.g., all photosynthetic pigments including chlorophylls versus photo-protective carotenoids (not shown). Phycobilins became increasingly important for cyanobacteria and cryptophytes under dim-light conditions and narrow spectral range. Gervais (1997b) concluded from experiments on light-dependent growth and dark survival that acclimatisation to low-light environment is an important pre-adaptation for the dominance of *Cryptomonas* species near the chemocline. Light acclimatisation below the compensation point to dim-light stimulates uptake of organic compounds in *Planktothrix rubescens* as indicated by in situ experiments on photo-heterotrophy by Zotina, Köster & Jüttner (pers. comm.). Both *Cryptomonas* and *Planktothrix* contribute to the deep chlorophyll maximum by active growth rather than by migration or sinking of cells, or depth-adjustment of filaments respectively (Gervais, 1997a; Bright & Walsby, 2000). The distinct carotenoid ratio PSC:PPC between 2–7 m and 10–12 m referred therefore mainly to the distinct phytoplankton composition between euphotic layer and the metalimnetic layer below 1% light intensity and did not show in detail the acclimatisation to underwater light climate (e.g. Descy et al., 2000; Teubner et al., 2001).

Mixing in both spring and autumn led to comparable low species similarities, indicating the same rapid change of species/rapid shift of individual biovolumes during rapid nutrient turnover. During stratification, the only two layers which were significantly different

in terms of change in species composition were 5 m and 12 m. These layers were representative for the two extreme conditions in the vertical, the epilimnetic euphotic zone with significant response to sunshine duration and the metalimnion below the euphotic zone with dim-light less than 1%, respectively.

Reynolds (1993) and Padišák (1994) supposed that a near-equilibrium state at environmental constancy requires 12–16 generations spanning 35–60 days in summer. Calculating the Bray-Curtis similarity measure from monthly intervals implies integration over several generations. Doubling times estimated from maximum growth rates under laboratory conditions range from 3.3 days in slow growing species such as *Ceratium hirundinella* to 1/2 day in fast growing unicellular diatoms. The doubling time of 2.8–5.3 days for a mixture of *Cryptomonas* measured by in situ growth rates in a deep living population (Gervais, 1998) was much longer than the 0.85 days expected from culture experiments (Morgan & Kalff, 1979). Similarly, a natural metalimnetic population of *Planktothrix rubescens* in Lake Zürich had doubling times of 7 days (Zotina, Köster & Jüttner, pers. comm.) compared to 1.7 days in culture (Meffert, 1971). We can therefore expect that this species has at least 4 generations during a monthly interval, while for most other species 30–75 generations can be expected (Reynolds, 1984). The dominance of individuals with long generation time, as we can expect for species in the metalimnion below the euphotic zone, implies a low change between the individual biovolumes of species, hence high Bray-Curtis similarities, if no other factors disturb the constancy of phytoplankton composition.

Significant relationships between zooplankton and phytoplankton in the epilimnetic layers substantiate this zone as homogeneous. Although only three species made up 80% of biomass at times, fluctuations within the community remained large. Judging from the small vertical migration amplitude of zooplankton in Ammersee (Morscheid & Mayr, 2002), separate impacts can be ascertained for epi- and metalimnion (Lampert, 1992; Adrian et al., 2001). Zooplankton had very little effect on phytoplankton species assemblages in the metalimnion while parameters related to stratification such as z_{eu}/z_{mix} and the Schmidt stability as well as those of trophic (TP, Chl) correlated with species changes.

To summarise, we defined steady state conditions in lake Ammersee as a stable community in terms of species composition and standing crop. Both aspects of stability in phytoplankton are shown in Figure 7.

The stability of species composition was measured by Bray-Curtis similarity between monthly samples. The 'perfect' equilibrium state measured by Bray-Curtis similarity is theoretical given by the value 1 (given as percentage it is equal to 100%), and would indicate no change of individual biovolumes of species from month to month. The stability of standing crop was evaluated by the net change of total biovolume from month to month. The 'perfect' equilibrium state in terms of standing crop is given by net change values of zero, means no increase or decrease of biomass, a perfect balance between production and losses. The definition of a steady state assemblage on both ends holds true only for metalimnetic layers at light levels below 1% in Ammersee. High values for similarity of phytoplankton composition of more than 80% are reached at almost zero net changes of phytoplankton. In contrast, similarity indices from all the euphotic layers never reached 60% and were usually significantly lower even if biovolume net changes were around zero. This result confirmed non-steady state assemblages at the epilimnetic layer in other deep lakes (e.g. Dokulil & Teubner, 2003; Salmaso, 2003) and the hypothesis that steady state conditions occur less regularly in deep lakes and are less predictable compared to surface layers in shallow polymictic lakes (Mischke & Nixdorf, 2003; Nixdorf et al., 2003).

The arched-shaped pattern in Fig. 7 implies that the lowest changes of species composition can be assumed at zero net change rates of total biovolume. The similarity of species composition between consecutive monthly samples at both layers, the epilimnion and the metalimnion, however, did not exceed 60 and 80% respectively. Hence the internal structure of plankton community altered even if no changes on higher level of aggregation were measured, a sign for compensatory changes in species populations within a community. It supports the idea by Scheffer et al. (2003), that plankton dynamics at higher level of aggregation, such as e.g. the total biovolume, are more predictable than on species level.

Conclusions

Steady state assemblage defined as a stable community hold true on both ends, a stable composition by low changes of individual biovolumes of species (Bray-Curtis) and stable standing crop by no net changes of total phytoplankton biovolume for metalimnetic layers at light levels below 1% in Am-

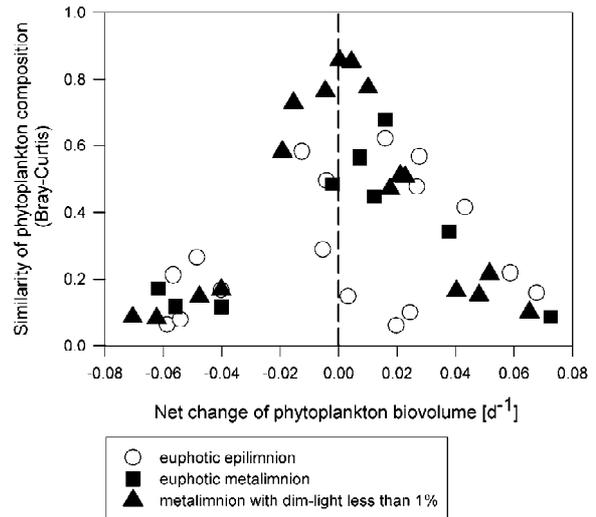


Figure 7. Relationship between the similarity of species composition (Bray-Curtis as measure for the change of individual biovolumes of species from month to month) and the net change of biovolume for the phytoplankton in the euphotic epilimnion (2 and 5 m), the euphotic metalimnion (7 m) and the metalimnion below the euphotic zone with dim-light less than 1% (10 and 12 m).

mersee. No steady state assemblages, however, were found for the euphotic layer. Focussing on phytoplankton composition these findings were further substantiated by relationships between Bray-Curtis similarities and environmental-biotic parameters. Stable phytoplankton composition in the metalimnion below 1% light intensity was associated with the increase of thermal water stability, high TP and with times when the three dominant species contributed more than 80% of total phytoplankton. No statistically significant influence of zooplankton biomass on species changes was observed in the metalimnion. Therefore the metalimnetic plankton community below 1% light can be seen as bottom-up controlled. The ratio of photosynthetic versus photoprotective carotenoids functionally related to the duration of sunshine throughout the year suggests, that the euphotic layer (≤ 7 m) can be seen as a homogenous community of photosynthetic organisms. The change of species in this euphotic layer was not significantly related to thermal stability, TP or the dominance structure of phytoplankton, but linked with the zooplankton biomass and therefore seemed to be top-down controlled. From our observations, we can conclude that only during stratification, and only in the metalimnion below the euphotic zone, can steady state assemblages be expected in the deep mesotrophic Ammersee.

pages 63-64 not shown

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