

Steady state of phytoplankton and implications for climatic changes in a deep pre-alpine lake: epilimnetic versus metalimnetic assemblages

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Introduction

The thermodynamic term 'steady state' originally coined by studies on chemical reaction kinetics is also used to define growth in continuous culture systems. It is also used to describe the persistence of biota and relatively stable conditions as a whole in an ecosystem such as the rain forest or parts of the ocean (SOMMER 1985, DOKULIL & TEUBNER 2003, NASELLI-FLORES et al. 2003).

According to SOMMER et al. (1993) three criteria must be met to consider a phytoplankton community to be in steady state: (1) no more than three species contribute >80% to the total biomass, (2) the persistence of these species for more than 1–2 weeks and (3) during this period the total biomass does not significantly change.

In the present study, we searched for time periods and depth layers in which phytoplankton steady states are most likely. We defined a steady-state phytoplankton assemblage as a stable community in terms of species composition (Bray-Curtis similarity) and standing crop (net change of total biovolume). We compared three spatially heterogeneous environments for vertical niche separation within the top 12 m in the dimictic pre-alpine Ammersee (Bavaria, Germany): the euphotic epilimnion, the euphotic metalimnion, and the metalimnion below the euphotic zone with light < 1% of the surface. We evaluated the applicability of the definition of steady state assemblages given above and discuss results with respect to environmental parameters and climatic change.

Key words: steady state, climate change, phytoplankton assemblages, pre-alpine lake

Methods

Ammersee is a mesotrophic, dimictic pre-alpine lake near Munich (Bavaria, Germany) with a maximum

depth of 81 m and a water volume of 1 750 106 m³. Further details on morphometry and trophy are described in TEUBNER et al. (2004).

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, 10 and 12 m was estimated from microscopically counted abundance and size measurements of single cells or colonies. Samples for pigments and chemical parameters were taken from 0, 2, 5, 7, 10, 12, 15, 20 and 30 m. The correspondence between vertical profiles of single species and of marker pigments species is in detail described in TEUBNER et al. (2003).

Photosynthetically active radiation (PAR) was measured with a 4 π quantum sensor (LI-COR). Underwater-light profiles were used to define the layer of 1% surface light intensity calculated from the vertical attenuation coefficient (Fig. 1). The mixing depth (z_{mix}) was calculated from the depth with maximum relative thermal resistance (RTR) against mixing by individual temperature profiles (WETZEL 2001), the heat content and the stability of stratification in the water column was calculated by using Schmidt stability according to LIVINGSTONE & SCHANZ (1994). The metalimnetic layer (Fig. 1), defined as the water stratum of steep thermal gradient demarcated by an almost homiothermal epilimnion and hypolimnion (WETZEL 2001), was calculated by RTR-values and was on average about 7.5–13 m for Ammersee in 2001.

The phytoplankton dissimilarity measure between each pair of successive monthly samples was based on continuous data (biovolumes of individual species). These dissimilarity values were calculated by Bray-Curtis ranging from 0 to 1 using SYSTAT. For easier interpretation the dissimilarity (d) was converted to similarity (s) by $s = 1 - d$. This similarity considers the biovolume of all individual species with > 3% contribution to total biovolume at a single

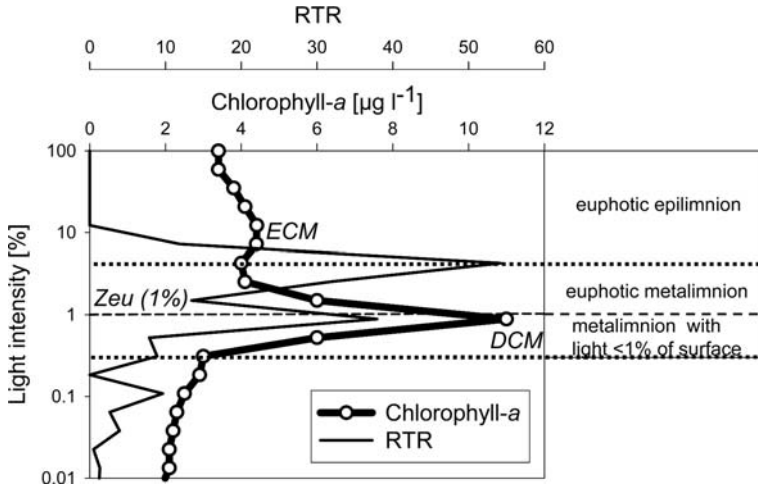


Fig. 1. Thermal stratification and vertical distribution of chlorophyll-*a* along the light gradient in July in Ammersee. The metalimnion layer is shown by dotted lines following RTR-values (WETZEL 2001), the euphotic zone by a light intensity > 1%. Chlorophyll-*a* was abundant in all three layers: the euphotic epilimnion, the euphotic metalimnion and the metalimnion with < 1%. The epilimnetic chlorophyll maximum (ECM) is related to 10% light, the deep chlorophyll maximum to about 1% light.

depth ($n = 80$), including nonobligate autotrophic taxa such as *Gymnodinium helveticum*. Net change of phytoplankton biomass $k_p = \frac{\ln p_2 - \ln p_1}{t_2 - t_1}$ as d^{-1} was calculated in the same time-intervals as Bray-Curtis similarity.

Results

A taxonomic list of the phytoplankton species, along with light micrographs and detailed descriptions of the flagellates, the vertical distribution pattern of algal species, chlorophylls and specific carotenoids present in the dimictic pre-alpine Ammersee for the year 2001, are given in detail in TEUBNER et al. 2003. Among 83 identified taxa, dominant species alternated seasonally and reached significant biovolumes 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 *Rhodomonas minuta*). A deep chlorophyll maximum, mainly by *P. rubescens*, was common in this deep mesotrophic lake. During summer stratification from 1997 to 2001, the

metalimnetic phytoplankton below the euphotic zone reached biovolumes that were on average 30% higher than those in the epilimnion (TEUBNER et al. 2004).

As an example of thermal stratification with multiple thermoclines and the deep chlorophyll maximum (Fig. 1), we distinguished three spatially heterogeneous environments for vertical niche separation within the top 12 m: the euphotic epilimnion represented by the 2 and 5 m samples; the euphotic metalimnion around 7 m; and the metalimnion below the euphotic zone with dim-light < 1% (10 and 12 m sample).

Both aspects of steady state phytoplankton assemblages defined in the introduction are shown (Fig. 2). 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, represented by the value 1 (as percentage 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 one month to the next. The “perfect” equilibrium state in terms of the

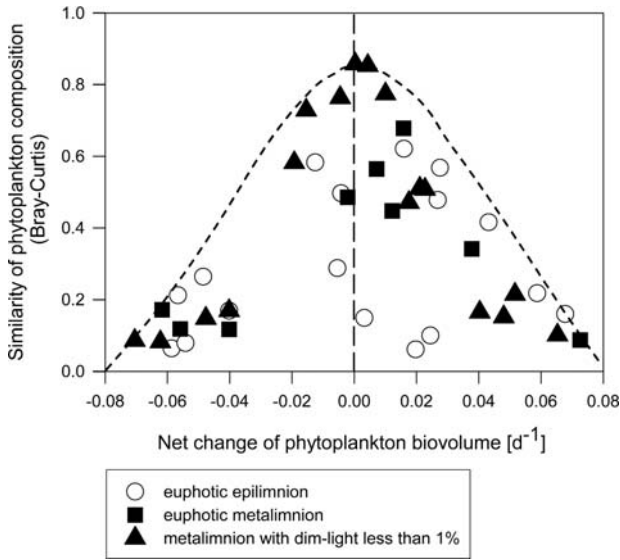


Fig. 2. Relationship between the similarity of species composition (Bray-Curtis as measure for the change of individual biovolumes of species from month to month) and the net change of biovolume for the phytoplankton (same time-intervals as for Bray-Curtis) in the euphotic epilimnion (2 and 5 m), the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

standing stock is given by net change values of zero, and indicates no increase or decrease of biomass (i.e. a balance between production and losses). The definition of a steady state assemblage on both ends hold true only for metalimnetic layers at light levels below 1% in Ammersee. High values for similarity of phytoplankton composition of > 80% are reached at almost zero net changes of phytoplankton. The greater the contribution of *P. rubescens* > *C. hirundinella* > unicellular centric diatoms > *A. formosa* > *Fragilaria* spp. > *A. lemmermannii* > *P. lenticularis* > *R. minuta* to biovolume at metalimnetic depths below the euphotic zone, the higher the Bray-Curtis similarities. In contrast, similarity indices from all euphotic layers never reached 60% and were usually significantly lower, even if biovolume net changes were around zero.

Findings emphasise the nonlinear relationship between the change of species composition and the change of standing crop (Fig. 2 and 3A and B). The change of species at the three depth layers was specifically different throughout the year (Fig. 2A). In contrast, the time series of the net change rates of phytoplankton biovolume revealed a coherent decreasing trend in all three layers. The two physical parameters, Schmidt stability (B-D, Fig. 3) and heat content

(F-H, Fig. 3), integrate temperature effects over the whole water column. Both parameters can be used as indicators of climatic changes. Values of Bray-Curtis similarity only corresponded well to thermal stratification at the metalimnetic dim-light layer. Highest values of similarity, which means almost no changes in species composition of the metalimnetic layer, were only reached during periods of stable stratification. The net change rates of phytoplankton at all three depth layers corresponded to the heat content (Fig. 3 F-H), the mean water temperature and the temperature of the respective strata. In a previous study (TEUBNER et al. 2003) we were searching for relationships between the change of species composition and trophic interaction or environmental parameters, respectively. At all sampling depths within the euphotic zone (≤ 7 m) the Bray-Curtis similarity was significantly related only to the biovolume of zooplankton (rotifers and metazoan zooplankton at 2 m $R = 0.73$, at 5 m $R = 0.60$, and at 7 m $R = 0.65$; $P < 0.05$). We found the opposite indication for the metalimnetic zone below the euphotic depth, 10 and 12 m, which were significantly related to all parameters (ratio of euphotic depth to mixing depth, Schmidt stability, concentration of chlorophyll-*a*) except zooplankton.

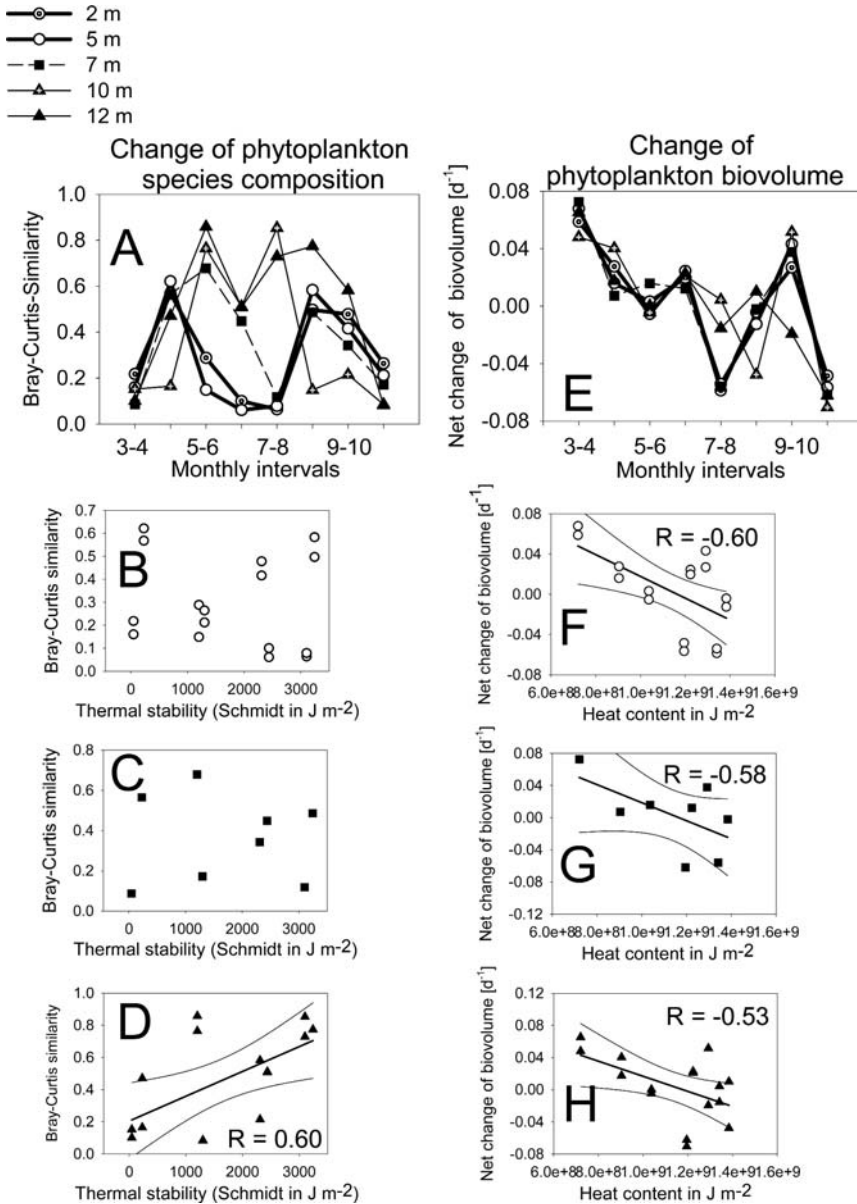


Fig. 3. Time series for the change between two successive monthly samples of both the species composition (A, as Bray Curtis) and the biovolume (E, as net change rates) in the euphotic epilimnion (2 and 5 m), the euphotic metalimnion (7 m) and the metalimnion below the euphotic zone with dim-light less than 1% (10 and 12 m). The relationship between Bray-Curtis-similarity and thermal stratification (Schmidt stability, B-D) and the heat content (F-H) and net changes respectively is separately shown for the three layers. Schmidt stability and heat content as means between successive monthly data.

Discussion

A steady state assemblage defined as a stable community in terms of species composition and standing crop was verified only for the metalimnetic layer with light < 1% of the surface level. At this dim-light layer > 80% similarity in phytoplankton composition was reached between successive monthly samples, associated with almost zero net changes of total biovolume. Such steady state assemblages in the microbiological sense could exist only if production and losses were perfectly balanced over time.

Differences in vertical niche separation between strata in Ammersee were pronounced by relative changes in species composition (Bray-Curtis). The steady state in the euphotic layer was not reached because of grazing, as indicated by the significant relationship between the Bray-Curtis similarity and the biovolume of zooplankton. Further, a previous study (TEUBNER et al. 2003) showed that most of the abiotic factors that have a major influence on phytoplankton dynamics were strongly fluctuating in the surface layer, therefore favouring higher dynamics in species change in the surface than in metalimnetic layers.

In contrast to changes of species composition, net change rates revealed a temporal coherence pattern between depth layers. Negative values of net change rates represent a decrease of phytoplankton biovolume due to lower primary production and/or relative higher losses. Periods of negative net change rates at all depths were significantly related to periods of seasonally higher temperature. These results imply that under conditions of a warmer climate, and hence longer thermal stratification of about 15 days per decade in Ammersee (TEUBNER et al. unpubl.), periods of negative net change rates will increase, indicating a relative enhancement of losses over primary production. In addition, we can expect that steady state periods in metalimnetic dim light layers (e.g. zero net changes of phytoplankton biomass associated with no changes of the species composition in deep layers) will be prolonged.

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References

- DOKULIL, M.T. & TEUBNER, K., 2003: Steady state phytoplankton assemblages during thermal stratification in deep alpine lakes. Do they occur? – *Hydrobiologia* **502**: 65–72.
- LIVINGSTONE, D.M. & SCHANZ, F., 1994: The effects of deep-water siphoning on a small, shallow lake: a long-term case study. – *Arch. Hydrobiol.* **132**: 15–44.
- NASELLI-FLORES, L., PADISÁK, J., DOKULIL, M. & CHORUS, I., 2003: Equilibrium/steady state concept in phytoplankton ecology. – *Hydrobiologia* **502**: 395–403.
- SOMMER, U., 1985: Comparison between steady state and non-steady state competition: Experiments with natural phytoplankton. – *Limnol. Oceanogr.* **30**: 335–346.
- SOMMER, U., PADISÁK, J., REYNOLDS, C.S. & JUÁSZ-NAGY, P., 1993: Hutchinson's heritage: the diversity-disturbance relationship in phytoplankton. – *Hydrobiologia* **249**: 1–7.
- TEUBNER, K., MORSCHIED, H., TOLOTTI, M., GREISBERGER, S., MORSCHIED, H. & KUCKLENTZ, V., 2004: Bedingungen für Auftreten toxischer Blaualgen (Cyanobakterien) in bayerischen Seen und anderen stehenden Gewässern. – *Materialien Nr. 113 Bayerisches Landesamt für Wasserwirtschaft, München*: 105 pp.
- TEUBNER, K., TOLOTTI, M., GREISBERGER, S., MORSCHIED, H., DOKULIL, M.T. & MORSCHIED, H., 2003: Steady state in a deep pre-alpine lake: species and pigments of epilimnetic versus metalimnetic assemblages. – *Hydrobiologia* **502**: 49–64.
- WETZEL, R.G., 2001: *Limnology: Lake and river ecosystems*. – Academic Press, 1006 pp.

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