Light, stratification and zooplankton as controlling factors for the spring development of phytoplankton in Lake Constance

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ABSTRACT

The patterns of phytoplankton growth and decline during the spring bloom and the following clear-water phase in Lake Constance have been studied on the basis of cell counts with short-term sampling intervals and related to light climate, stratification and zooplankton pressure.

Introduction

The outburst of the phytoplankton spring bloom and the subsequent clearwater phase is a well-known pattern in the seasonal periodicity of phytoplankton in Lake Constance. Its regularity has been shown by Geller [2]. The breakdown of phytoplankton biomass at the beginning of June has been attributed to zooplankton grazing [7]. The algal species composition in the spring phase has been very predictable within the last years [11, 12]; information on long-term trends in phytoplankton development is available from Bürgi [1]. With the exception of Lampert and Schober [7] most of the data available on Lake Constance spring bloom are based on weekly sampling, which is not completely adequate for a period, in which 10-fold increases and decreases of biomass can be observed. Lampert and Schober's [7] study put the emphasis on zooplankton and did not analyze phytoplankton dynamics on the species level. Therefore it was attempted here, to study the development of the dominant phytoplankton species on the basis of cell-count data with very short sampling intervals and to relate the patterns of growth and decline to the supposed controlling factors stratification, light and zooplankton pressure. In total the results of 38 sampling events from the end of March until the end of June 1981 are discussed here.

Methods

Samples were taken from the deepest point of 'Überlinger See', a 147 m deep northwestern bight of Lake Constance, at 0, 1, 2, 3, 4, 5, 6, 8, 10, 12.5, 15, 17.5, 20, 25, 30, 40, 50, 70, 100 and 140 m dephts. Subsamples for cell counts were immediately fixed by Lugol's iodine solution. Mixed samples representative for the 0–5,

5-10, 10-15, 15-20 and 20-140 m were allowed to settle in 50-ml Utermöhl chambers and counted with the inverted microscope. At least 400 individuals of the dominant and 100 individuals of the subdominant species were counted. Thus a counting accuracy of roughly ±10% for the dominant species could be achieved. The linear dimensions of 100 individuals of the dominant and 40 of the subdominant species were measured to calculate cell volumes according to the recommendations of Rott [10].
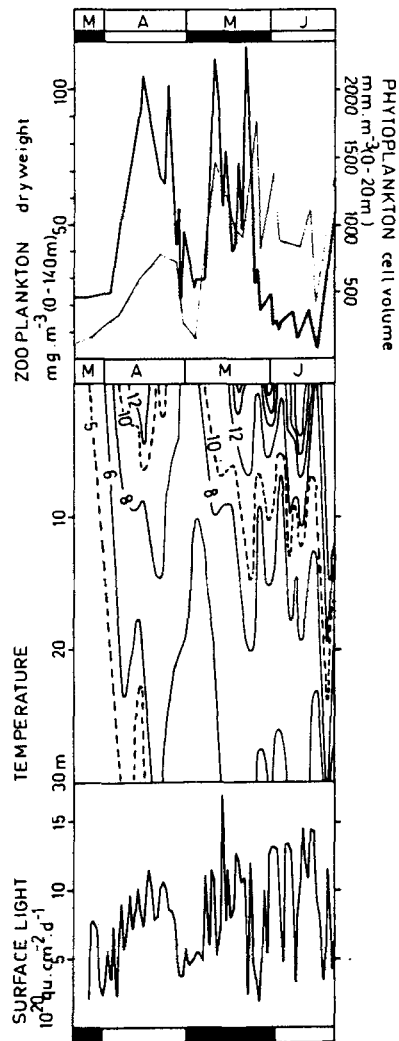

Figure 1. Top: Phytoplankton and zooplankton biomass in Lake Constance during the spring phase 1981. Phytoplankton: thick line, cell volume ($mm^3 \cdot m^{-2}$; integrated from 0 to 20 m).
Zooplankton: shaded area, dry weight ($mg \cdot m^{-3}$; average from 0 to 140 m).
Middle: depth-time diagram of water temperature.
Bottom: surface irradiance (10^{20} quanta$\cdot cm^{-2} \cdot d^{-1}$).

Temperature was measured with a Züllig-Baerlocher 'hydropolytester' multiprobe and underwater light intensity with a quantum scalar irradiance meter (Biospherical Instruments). Surface irradiance was continuously recorded by a similar light meter situated on the roof of the limnological institute of Constance university.
The zooplankton dry weight data were kindly supplied by Dr. W. Geller, who took samples with a Clarke-Bumpus sampler.

Results

The onset of thermal stratification could be observed at the end of March. It was followed by explosive growth of phytoplankton (fig. 1). Some species (*Rhodomonas lens, Rhodomonas minuta, Cryptomonas ovata,* see fig. 2) grew already from 26 March to 3 April; a marked increase of the total phytoplankton crop could not be observed before 7 April, because the remaining populations of winter plankton *(Asterionella formosa, Stephanodiscus astraea)* formed a background large in comparison to the species now starting growth. At the end of April a period of bad weather lead to a partial destratification of the lake. Surface temperature decreased from 13.5 °C on 14 April to 6.5 °C on 5 May. The temperature difference from the surface to 20 m depth fell from 8.4 °C to 0.6 °C. The bad weather period is not only shown by the depth-time diagram of the temperature but also by the time course of daily surface irradiance (fig. 1). Phytoplankton biomass (= cell volume) decreased to the same level as in March. In the following time surface irradiance increased again, the surface water warmed up and the lake stratified again. Soon a second growth pulse of phytoplankton could be observed, yielding crops that were even higher than in April. The growth of phytoplankton was quickly followed by an increase of zooplankton biomass. Both phyto- and zooplankton had a minor depression in mid May. A rapid decrease in phytoplankton concentrations at the end of May lead to the well-known 'clear-water phase'. Zooplankton crops remained fairly high during that phase, that lasted until the second third of June.
As in the previous years spring bloom phytoplankton in Lake Constance was dominated by four species: *Rhodomonas lens, Rhodomonas minuta, Cryptomonas ovata, Stephanodiscus hantzschii* (probably including some other small centric diatoms). Even the accessory species were the same as in 1979 and 1980: *Cryptomonas marssonii, Erkenia subaequiciliata, Monoraphidium contortum, Elakatothrix gelatinosa, Chlamydomonas* spp. and 'µ-algae' (probably *Chlorella* sp. and small blue-green algae); during the April growth phase also *Asterionella formosa* and *Stephanodiscus astraea* were of some importance. Except for the latter two, which grew only in April, all species had the same bimodal growth pattern as total biomass. Only *Cryptomonas ovata* had a continuous period of increase during the clear-water phase, after it had declined rapidly at the end of May like the other species (fig. 2B).
The growth curves both of total phytoplankton and of the single species (fig. 2A and B) showed considerably irregular fluctuations, that exceeded the counting error. These fluctuations are probably not only due to real processes of growth and loss, but also to horizontal heterogeneity in phytoplankton distribution and to the fact, that sampling was not always performed at the same time of the day. In the majority of cases samples were taken at 8.00 mid-European time, but sometimes also at 18.00. Several processes like photosynthesis, grazing by vertically migrating zooplankton
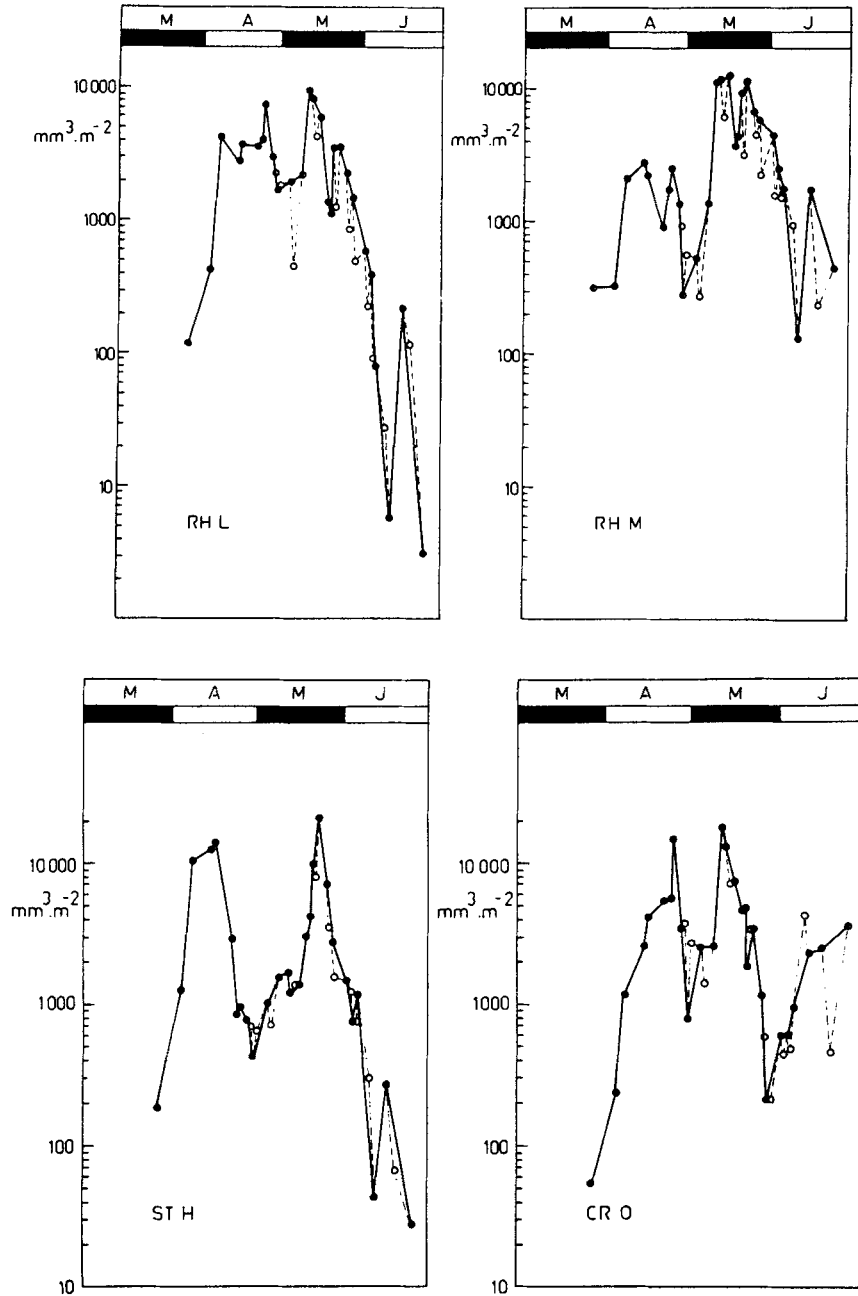
Figure 2. A: Biomass (mm³·m⁻²; integrated from 0 to 20 m) of *Rhodomonas minuta* (RH M) and
Rhodomonas lens (RH L).
Full circles: morning samples. Empty circles: evening samples.
B: Biomass of *Cryptomonas ovata* (CR O) and *Stephanodiscus hantzschii* (ST H).

species and possibly phased cell division of algae [4] have a diurnal pattern and make comparison between morning and evening samples of different days difficult. It can be seen from figure 2 that exclusion of the data taken from afternoon samples makes the growth curves much smoother and eliminates a great part of the unregular variation. Therefore only the morning values shall be taken into consideration for the following conclusions.

Discussion

It shall be attempted here, to explain the observed patterns of increase and decrease by the predominant influence of a single growth factor and a single loss factor: light and zooplankton pressure. Mohammed and Müller [8] and Lampert and Schober [7] have also mentioned phosphorus limitation as possible factor controlling algal growth at the height of the spring bloom. The minimum concentration for dissolved reactive phosphorus during the spring bloom was 11 µg $P \cdot l^{-1}$ on 27 May as average concentration from 0 to 6 m (Stabel; unpublished data). This is in good agreement with the observations from previous years [14], which also do not indicate severe limitation of algal growth by phosphorus during the spring bloom. Most values given in the literature for half-saturation constants (K_S) of phosphorus limited
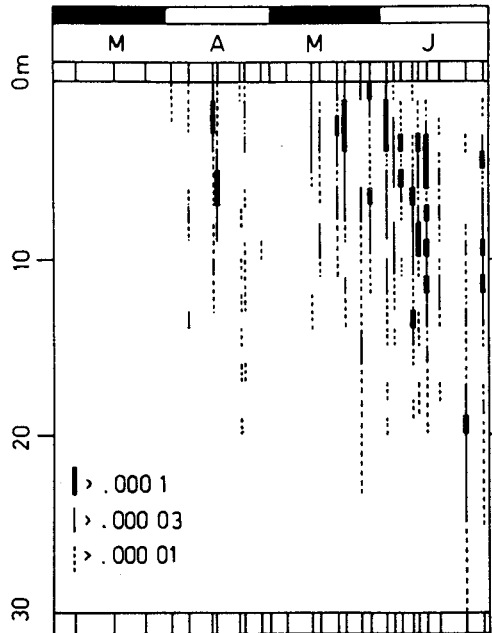
Figure 3. Gradient of density from meter to meter.
Thick line: gradient >0.0001 m^{-1}. Thin line: gradient 0.00003 to 0.0001 m^{-1}. Broken line: gradient 0.00001 to 0.00003 m^{-1}.
The vertical marks on top and bottom of the diagram indicate the days, when temperature profiles have been taken.

growth are below 5 $\mu g \cdot l^{-1}$. Furthermore it has to be considered, that during the spring bloom never algal crops as high as in summer are reached [11], although the concentrations of total phosphorus in the euphotic zone are much higher in the spring bloom (>60 $\mu g \cdot l^{-1}$) than in the time of summer biomass maxima (<20 $\mu g \cdot l^{-1}$). This probably means a much higher intracellular P-concentration during the spring bloom, which could support further growth, even if external supply of phosphorus slows down. Therefore I conclude, that phosphorus limitation plays only a minor role during the spring development of phytoplankton.

The main importance of temperature is an indirect one: stratification and water column stability have considerable consequences to the 'effective light climate' [9] to which algae are exposed. In the period under study Lake Constance did not develop the classical pattern of thermal stratification with a homothermic epilimnion, a thermocline and a hypolimnion. The temperature gradient usually had a quite irregular pattern in the upper 30 m. Figure 3 gives the gradients of density, transformed from temperature data according to the table from Hutchinson [6]. The gradient of density is more relevant for water column stability than the temperature gradient. The zones of the strongest density gradients can be considered as mixing barriers. It can be seen from figure 3 how the bad weather period at the end of April and beginning of May led to a nearly complete destruction of these mixing barriers. During the second phase of the spring bloom and the clearwater phase the water column remained fairly stable. Much of the upward and downward shifts of the zones of density gradients is probably due to internal seiches, which have been shown to be very important in Lake Constance by Hollan and Simons [5].

The light intensity to which algal populations are exposed depends on surface irradiance, water transparency and the depth distribution of the population, which is influenced by water movements, sedimentation and in some cases vertical migration [13]. Ramberg [9] has defined the 'effective light climate' as the average light intensity in the mixed water layer.

$$\bar{I} = \frac{I_0 (1 - e^{-\varepsilon z_m})}{\varepsilon z_m}$$

I_0: surface light intensity
ε: extinction coefficient
z_m: mixing depth
$\bar{I}$: effective light climate

This equation is not directly applicable to situations without mixed epilimnion or with an epilimnion, that is much thinner than the extension of algal productivity. For that case I propose a slight modification:

z_{50} instead of z_m: median depth of an algal population, where 50% of it are above and 50% are below.

$\bar{I}_{50}$ instead of $\bar{I}$: average light intensity from the surface to the median depth of a population, 'species specific effective light climate'.

This modification has the additional advantage of taking interspecific differences in the depth distribution into account. $\bar{I}_{50}$ for the dominant species is given together

with I_0 and ε in the table. From the data given it is obvious, that the breakdown of phytoplankton at the end of April is caused by destratification and transport of algae into the dark, deep zones of the lake. The decrease of $\bar{I}_{50}$ is by far stronger than the decrease of surface irradiance.

The phytoplankton breakdown at the end of May has been shown by Lampert and Schober [7] and Geller [2] to be caused by zooplankton grazing. During the whole breakdown period and the subsequent clearwater phase there was no destratification comparable to the end of April, surface irradiance varied mostly between medium and high values, the extinction coefficient of the water is low and nutrients are in abundant supply, as far as we know from the previous years. In spite of these near to optimum growth conditions phytoplankton crops remain low during the clearwater phase. Three of the four species, *Rhodomonas lens, Rhodomonas minuta, Stephano-discus hantzschii* are in the optimum size range of particles ingestible for the dominant zooplankton species *Daphnia hyalina* and *Daphnia galeata*. The longest linear dimensions are well below 30 µm, which is considered roughly to be the upper size limit for edible particles [3]. *Cryptomonas ovata* is just above this limit as far as the cell length is concerned (35 ± 8 µm), but the width of the cells is well below this limit and it should be at least edible for adult *Daphnia*. Maybe the slow, but continuous increase during the clearwater phase is due to a slightly reduced edibility for juvenile zooplankton.
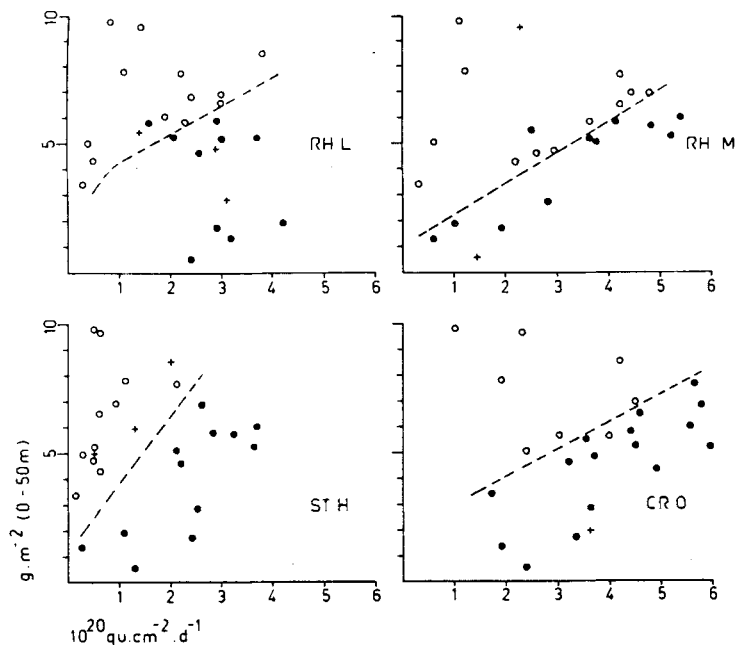
Figure 4. Zooplankton and light as controlling factors for phytoplankton growth.
● = significant increase, ○ = significant decrease, + = no significant change. y-axis: zooplankton dry weight (g·m^{-2}; integrated from 0 to 50 m). x-axis: effective light climate ($\bar{I}_{50}$; 10^{20} quanta·cm^{-2}·d^{-1}). Broken line: equilibrium line, separating the fields of increase and decrease. Abbreviations for species as in figure 2.

The hypothesis, that the patterns of increase and decrease of phytoplankton populations are predominantly controlled by light and zooplankton pressure during the period under study, shall be tested by a simple graphical method (fig. 4). The intervals between samples are grouped into three categories: significant increase, significant decrease and intervals without significant population density change. Changes are considered significant, when they either exceed a factor of 2 or they extend over a continuous series of at least 3 data points. The points representing the classified sampling intervals are plotted into a field, were the x-axis represents the growth factor (light) and the y-axis the loss factor. If the hypothesis is right, there should be a field of points representing increase nearer to the x-axis and a field of decrease nearer to the y-axis. The growth factor is defined as $\bar{I}_{50}$, the loss factor as zooplankton dry weight. This is only a very rough estimate of zooplankton pressure, which does not take into account different activities of different species and different age classes. In spite of this rather unsatisfactory definition of the loss factor, it is possible to draw an 'equilibrium' line, which separates the fields of increase and decrease. Only 3 out of 93 data points are situated in the 'wrong' field, which is considered a good proof of the hypothesis mentioned above.

Unfortunately there are only few points close to the equilibrium line, whose slope therefore is not well defined. It is therefore difficult to recognize interspecific differences, with the exception of *Stephanodiscus hantzschii*, whose equilibrium line is markedly steeper. Since *Stephanodiscus hantzschii* is probably equally submitted to grazing as the *Rhodomonas* species, this difference is probably caused by smaller light demands. As a nonflagellate species *Stephanodiscus* is submitted to sedimentation and is not able to migrate upwards, if light is limiting. For a species of this type the ability to grow under low light conditions is obviously more important than for flagellates.

Summary

The phytoplankton dynamics in Lake Constance during the spring phase of 1981 have been studied on the basis of cell-number and cell-volume data taken from short-term sampling intervals. It is attempted to explain the patterns of increase and decrease of the four dominant algal species *Rhodomonas lens, Rhodomonas minuta, Cryptomonas ovata, Stephanodiscus hantzschii* by the antagonistic influence of a single growth factor (light) and a single loss factor (zooplankton grazing). The effective light climate to which algae are submitted is not only controlled by surface irradiance and transparency of the water, but also by the extent of thermal stratification, which controls the depth distribution of algal populations. Rapid algal growth did not start, before the lake became stratified at the beginning of April. A bad weather period at the end of April destratified the lake partially. Phytoplankton responded with a marked decrease in biomass. A second growth pulse could be observed when the lake stratified again. At the end of May heavy zooplankton grazing reduced algal crops to levels like before the spring bloom, leading to the well-known clearwater phase, that lasted until late June. By means of a simple graphical plot (fig. 4) it can be shown, that the antagonism of only two factors – light

and zooplankton pressure – is sufficient, to explain phytoplankton dynamics in the spring phase of Lake Constance. Consequently other environmental factors are of minor importance only.

ZUSAMMENFASSUNG

Licht, thermische Schichtung und Zooplankton als Kontrollfaktoren der Phytoplanktonentwicklung in der Frühjahrsphase im Bodensee

Die Phytoplanktondynamik im Bodensee wurde in der Frühjahrsphase 1981 auf der Basis von Zellzählungen und -volumina bei kurzen Probenabständen untersucht. Zuwachs und Rückgang der vier wichtigsten Phytoplanktonarten *Rhodomonas lens, Rhodomonas minuta, Cryptomonas ovata* und *Stephanodiscus hantzschii* (Abb. 2) sollten in zureichender Weise durch den antagonistischen Einfluss von nur zwei Faktoren erklärt werden: Licht und Zooplanktondruck. Das effektive Lichtklima, dem die Algen ausgesetzt sind, hängt nicht nur von der Oberflächeneinstrahlung und der Transparenz des Wassers, sondern auch von der thermischen Schichtung der Wassersäule ab, die die Tiefenverteilung der Algenpopulationen beinflusst. Schnelles Algenwachstum begann nicht vor dem Einsetzen der thermischen Schichtung Anfang April (Abb. 1). Eine Schlechtwetterperiode Ende April führte zu einem Abbau der Schichtung (Abb. 3) und in Kombination mit verringerter Oberflächeneinstrahlung zu einem Rückgang der Algenbiomasse. Ein zweiter Wachstumspuls konnte beobachtet werden, als der See wieder geschichtet war. Ende Mai führte starke Abweidung durch das Zooplankton zu einem Rückgang des Phytoplanktons auf ein Niveau wie vor der Frühjahrsblüte. Das nachfolgende Klarwasserstadium dauerte bis weit in den Juni. Mit Hilfe einer graphischen Methode (Abb. 4) konnte gezeigt werden, dass das antagonistische Wechselspiel von nur zwei Faktoren – Licht und Zooplankton – ausreicht, um die Phytoplanktondynamik im Bodensee während der Frühjahrsphase zu erklären. Daher spielen andere Umweltfaktoren in diesem Abschnitt nur eine untergeordnete Rolle.

RÉSUMÉ

Lumière, stratification et zooplancton comme facteurs de contrôle pour le développement printanier du phytoplancton dans le lac de Constance

La dynamique phytoplanctonique dans le lac de Constance a été étudiée pendant la phase printanière de 1981 sur la base du comptage des cellules et du volume cellulaire. On a essayé d'interpréter la croissance et la décroissance des espèces phytoplanctoniques les plus importantes, *Rhodomonas lens, Rhodomonas minuta, Cryptomonas ovata* et *Stephanodiscus hantzschii* (fig. 2), par l'influence antagonistique de seulement deux facteurs: lumière et prédation par le zooplancton. L'intensité lumineuse effective, à laquelle les algues sont exposées, dépend non seulement de l'intensité lumineuse superficielle et de la transparence de l'eau, mais aussi de la stratification thermique qui influence la distribution verticale des populations algales. Une croissance rapide des algues n'a pas débuté avant le commencement de la stratification thermique au début d'avril (fig. 1). Une période de mauvais temps, fin avril, a produit une destruction de la stratification de l'eau qui, en liaison avec une diminution de l'intensité lumineuse superficielle, a causé une décroissance de la biomasse algale (fig. 3). Après la restauration de la stratification du lac, un deuxième épanouissement phytoplanctonique a été observé. Fin mai, la forte prédation par le zooplancton a diminué la biomasse de phytoplancton au niveau d'avant la croissance printanière. La phase de l'eau claire suivante a duré jusqu'au deuxième tiers de juin. A l'aide d'une méthode graphique (fig. 4), il est démontré que l'antagonisme de seulement deux facteurs – lumière et zooplancton – est suffisant pour expliquer la dynamique du phytoplancton pendant la phase printanière. Pour cette raison, les autres facteurs de l'environnement sont de peu d'importance.

Light climate in Lake Constance, spring phase 1981. Surface light intensity (I_0; 10^{20} quanta·cm^{-2}·d^{-1}), extinction coefficient (ε; m^{-1}), species specific effective light climate ($\bar{I}_{50}$; 10^{20} quanta·cm^{-2}·d^{-1}).

Time	Mean I_0		Mean $\bar{I}_{50}$ for			
			R. lens	R. minuta	C. ovata	S. hantzschii
26.3.-3.4.	5.0	0.31	2.4	1.3	2.4	1.3
3.4.-7.4.	5.8	0.46	2.9	1.9	3.3	2.4
7.4.-14.4.	8.1	0.64	3.1	2.7	3.6	2.5
14.4.-15.4.	8.0	0.71	2.6	2.7	3.2	2.2
15.4.-21.4.	9.3	0.68	2.9	2.9	3.7	0.5
21.4.-23.4	10.3	0.63	3.7	3.6	4.5	0.5
23.4.-24.4.	9.4	0.63	3.0	3.7	3.3	0.5
24.4.-27.4.	7.5	0.54	0.4	0.6	2.4	0.3
27.4.-29.4.	4.1	0.41	0.3	0.3	1.7	0.15
29.4.-4.5.	5.0	0.33	3.3	0.7	1.9	0.6
4.5.-8.5.	6.5	0.33	4.4	1.0	3.6	1.1
8.5.-11.5.	8.5	0.59	2.9	4.1	3.0	1.3
11.5.-12.5.	6.2	0.75	1.4	2.3	2.3	0.6
12.5.-15.5.	10.3	0.66	3.8	4.4	4.2	2.0
15.5.-18.5.	10.3	0.55	2.4	4.8	4.5	2.6
18.5.-19.5.	12.5	0.64	1.9	5.6	5.6	3.7
19.5.-20.5.	11.4	0.81	1.6	4.8	4.0	3.2
20.5.-22.5.	8.7	0.85	1.4	2.5	3.5	2.1
22.5.-25.5.	5.7	0.71	1.1	1.2	1.9	1.1
25.5.-27.5.	3.1	0.61	0.8	1.1	1.0	0.5
27.5.-1.6.	9.9	0.58	3.0	4.5	4.8	0.7
1.6.-3.6.	11.7	0.54	3.0	4.4	5.8	0.9
3.6.-5.6.	7.7	0.43	2.3	3.6	4.4	2.8
5.6.-11.6.	10.7	0.35	2.2	4.2	5.7	2.2
11.6.-15.6.	13.3	0.28	1.6	5.2	6.0	3.6
15.6.-24.6.	7.8	0.30	0.5	2.2	4.9	0.7

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