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Lake Constance, Characterization of an ecosystem in transition

The impact of the interannual variability in hydrodynamic conditions on the plankton development in Lake Constance in spring and summer

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with 7 figures

Abstract: Long-term measurements (1979-1994) of meteorological parameters and of algal and crustacean biomass were used in conjunction with a comprehensive hydrodynamic model to evaluate the impact of the weather regime on plankton dynamics in a large, deep, temperate lake (Upper Lake Constance), and to identify potential causal mechanisms. The natural variability of weather conditions, including the exceptionally mild winters during the late eighties, allowed to investigate the covariation of meteorological parameters such as irradiance, air temperature, and wind with vernal algal and crustacean population growth. Crustacean zooplankton responded strongly to differences in surface water temperature, but not to mixing depth or algal biomass. Clear relationships between changes of algal biomass and meteorological factors were only found during the rare occasions when they acted together to favour or hamper algal development. Otherwise, the impact of the meteorological on the physical conditions, which were most likely conducive to phytoplankton development, could not be followed by this simple approach. This problem was overcome with a one-dimensional hydrodynamic turbulent exchange model driven by the meteorological boundary conditions at the water surface. It was used to simulate the development of the vernal density stratification and to study the relationships between meteorological parameters and exchange rates from the euphotic to the aphotic zone. The beginning of the spring algal bloom was shown to depend on the stabilization of the upper part of the water column. As soon as mixing below 20 m was inhibited, confining the algae to the euphotic zone for prolonged periods of time, substantial increases in algal standing stock occurred consistently. In contrast, during periods when high vertical mixing rates were computed with the model, no substantial enhancement of algal biomass was found. This tight coupling between the estimates of vertical mixing intensity and observed algal development, combined with knowledge about the impact of individual meteorological factors on mixing, enabled predictions about the response of algae to different weather conditions during spring.

Introduction

Hydrodynamic conditions and population dynamics of plankton organisms are influenced directly and indirectly by the meteorological regime in numerous ways (e.g., SCHINDLER et al. 1990, SEIP 1991, GEORGE & TAYLOR 1995, SEIP & REYNOLDS 1995). Consequently, changes in

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global circulation patterns and local weather conditions may have far-reaching consequences for pelagic ecosystems during the next few centuries (e.g. CARPENTER et al. 1993). For example, the onset of the phytoplankton spring bloom in the ocean and in deep temperate lakes is known to depend strongly on water column stability and, hence, on meteorological and hydrodynamic conditions (SVERDRUP 1953, ERGA & HEIMDAL 1984). Interannual variability of water temperatures in summer (MOORE et al. 1995) and winter (ADRIAN & DENEKE 1996, STRAILE & GELLER 1998a, b) markedly affect crustacean communities. However, quantification of the impact of single meteorological parameters on, e.g. vernal plankton development, has rarely been achieved. One way to improve our limited understanding of the potential reactions of pelagic food webs to changes in various meteorological patterns is to analyse the effect of their interannual fluctuations on hydrodynamic conditions and on the seasonal dynamics of different groups of pelagic organisms.

In late winter and early spring, phytoplankton in temperate, deep, non-ultraoligotrophic lakes such as Upper Lake Constance is commonly regarded as being regulated by physical factors (e.g., SOMMER et al. 1986, SOMMER 1987). During this period, grazing pressure on phytoplankton is low and nutrient concentrations reach maximum (non-limiting) values, whereas the average irradiance is still rather low (8-20 mol m^{-2} d^{-1} at Upper Lake Constance, TILZER & BEESE 1988) compared to typical summer values (around 40 mol m^{-2} d^{-1}). Light limitation is brought about by the large mixing depth which prevails under non-stratified conditions in deep lakes. The mean light intensity to which individual algal cells are exposed is reduced since residence times in the euphotic zone are short during homothermy (mean depth of Upper Lake Constance: 101 m, euphotic depth: around 22 m at maximum). Consequently, the onset of vernal algal development is thought to be triggered by a decrease in mixing depth (e.g., SOMMER et al. 1986, GAEDKE et al. 1998a, b). This implies that the persistence of high algal biomass over a long period of time requires an increase in water column stability in large and deep lakes such as Upper Lake Constance. The beginning of the spring phytoplankton bloom is quickly followed by a response of all consumer groups within the plankton (e.g. MÜLLER et al. 1991). Additionally, wintry weather conditions may have an especially marked effect on the dynamics of crustacean zooplankton (STRAILE & GELLER 1998a, b) and fish (ECKMANN et al. 1988) beyond the spring period.

It is difficult to measure turbulence in the water column directly, and its computation based on meteorological parameters demands sophisticated and reliable hydrodynamic models. Since turbulence is strongly influenced by irradiance, (air) temperature, and wind, we tried to employ these easily measurable parameters as indicators for the light history of algae and, hence, for the start of the spring bloom. However, correspondence may be weak given the complex effect of various current and past meteorological factors on mixing depth (GAEDKE et al., 1998a). The present study applies two different approaches, the qualitative comparison of time series and hydrodynamic modelling, to analyse the impact of weather conditions on plankton development in order to account for and to compare the advantages and limitations of both techniques. Firstly, fifteen consecutive years of temporally highly resolved investigations (1979-1993/94) of algal population dynamics are used to compare variations in irradiance, air temperature, and wind with those in algal biovolume. Furthermore, meteorological conditions prevailing during years in which the onset of the spring bloom was early are compared to those observed during years in which algal growth started normal or late. Secondly, water column stability and vertical mixing rates are derived from an elaborate hydrodynamic model (OLLINGER & BÄUERLE 1998) for 1987-94 and related to algal development in spring.

Especially the latter approach enables the impact of individual meteorological factors on water column stabilization and, thus, on the timing of the spring bloom to be evaluated. Finally, heterotrophic organisms at higher trophic levels of the food web with longer generation times and lower susceptibility to vertical mixing are considered by searching for relationships between weather conditions in winter and spring and the development of herbivorous and carnivorous crustacean zooplankton in spring and summer referring to 17 years of measurements (1979-95) with short sampling intervals.

Lower levels of aggregation such as individual organisms and species react generally more rapidly and more sensitively to external perturbations than entire communities do (e.g. ADRIAN & DENEKE 1996, GAEDKE et al. 1996, GAEDKE 1998a). For example, algal species composition is well known to depend, among other things, on the degree of turbulence (REYNOLDS 1984). This suggests focusing on individual species in order to evaluate the subtle effects of weather conditions. However, a better understanding of the functioning of pelagic communities first demands that major functional groups, i.e., higher levels of aggregation, be taken into account. The effect of meteorological factors on individual phytoplankton species will be analysed subsequently when model results on water column stability become available for all years of plankton investigations.

Lake Constance is presently undergoing re-oligotrophication and has changed from an approximately mesoeutrophic to a more oligotrophic state during the study period (1979-1995) (GÜDE et al. 1998). At the height of eutrophication, algal biovolume reached up to 50-100 cm^3/m^2 (GAEDKE 1998b) and maximum chlorophyll concentrations in summer remained below 20 µg/l (average over 0-20 m; HÄSE et al. 1998). Cyanobacteria were never important in Upper Lake Constance. In summer, algal biomass and taxonomical composition have responded to the reduced phosphorus concentrations. However, the onset of algal growth in spring is unlikely to be affected by the re-oligotrophication process because concentrations of all nutrients are sufficiently high to allow maximum growth rates during this time (GAEDKE & SCHWEIZER 1993, GAEDKE 1998b, GÜDE & GRIES 1998). Crustacean biomass and species composition have so far hardly exhibited any trends related to nutrient conditions (STRAILE & GELLER 1998).

Methods

Upper Lake Constance (in German: Bodensee-Obersee) is a large (472 km^2) and deep (z_{max} = 253 m), perialpine (47°39'N) lake of warm-monomictic character on the northern fringe of the Alps. As expected from its large size and depth, the stratification in Upper Lake Constance is on average less pronounced and less stable than that typically found in small and shallow lakes. During the period of stratification, the well-mixed epilimnion frequently extends down only a few meters and is followed by a thick (ca. 15-30 m) metalimnion characterised by gradually decreasing temperatures. Hypolimnetic temperatures are about 4-5 °C throughout the year, exhibiting some interannual fluctuations. Upper Lake Constance was never covered by ice during the period of investigation which has only occurred once during this century (for details see BÄUERLE et al. 1998).

Meteorological data (solar radiation, cloud cover, wind speed and direction, air temperature, humidity) were measured at the nearby meteorological station at Constance (German Weather Service). Vertical mixing intensity may depend more strongly on individual intense wind events, even if they last only for hours, than on the wind speed averaged over a longer period of time. To account for this fact, the potential impact of wind on changes of algal standing stocks was evaluated by first computing the third power of the hourly wind speed which reflects the wind energy flux from the atmosphere down to the air-water interface. These hourly estimates of wind energy fluxes were summed up for each day and then averaged. The third root of this value was then used as the daily average of the wind speed and related to algal population dynamics.

Field samples were taken weekly during the growing season and approximately biweekly in winter at different depths at a sampling site 147 m deep in the fjord-like north-western part of Upper Lake Constance (Überlinger See). Chlorophyll α was determined spectrophotometrically from hot ethanol extracts and corrected for phaeopigments by acidification applying the method of NUSCH (TILZER & BEESE 1988, TILZER et al. 1991, HÄSE et al. 1998). Algal biovolume was obtained by counting the abundance of individual species and morphotypes with the UTERMÖHL technique and allocating fixed cell volumes to each species (SOMMER 1987, GAEDKE & SCHWEIZER 1993, GAEDKE 1998b). Chlorophyll concentrations and algal biovolume covary closely in spring and are employed interchangeably as indicators of algal standing stock. For biovolume, a somewhat longer and almost uninterrupted time series is available, whereas measurements of chlorophyll provide a higher vertical resolution and a better indicator of the optical properties of the water. Crustacean zooplankton was sampled weekly during the growing season from 1979 onwards (no data in 1983) with a Clarke-Bumpus sampler (mesh size: 140 µm) (STRAILE & GELLER 1998). Biomass was calculated from relationships between length and dry weight established for Lake Constance (GELLER & MÜLLER 1985, WÖLFL 1991). Crustacean species were assigned to three guilds, i.e., predominantly herbivorous crustaceans (*Daphnia hyalina, D. galeata, Bosmina* spp., and *Eudiaptomus gracilis*), cyclopoid copepods, and carnivorous cladocerans (*Leptodora kindtii* and *Bythotrephes longimanus*).

By means of an improved version of a one-dimensional numerical κ–ε model (OLLINGER & BÄUERLE 1998), the turbulent transports of momentum, heat, and mass in the water column were simulated. These are induced by the direct influence of the wind at the lake's surface, by shortwave and longwave radiation, and by the fluxes of latent and sensible heat. It is assumed that the transport processes associated with turbulence may be described by turbulent exchange coefficients which are determined by means of two differential equations, one for turbulent kinetic energy, κ, and one for the dissipation, ε, of turbulent kinetic energy κ.

The eddy diffusivity, K_T (turbulent exchange coefficient for heat), is related to the eddy viscosity, μ_T (turbulent exchange coefficient for momentum), with the aid of a turbulent Prandtl number, σ_T, which is taken to be 1.0 in this study (for further details of the turbulence model, see SVENSSON 1978). Given the meteorological conditions at the water surface, the temporal and vertical distributions of μ_T and K_T are calculated, thus, allowing the turbulent state of the water column to be determined. In order to gain information about the light history of plankton cells floating in the turbulent water column, it is necessary to convert μ_T into random vertical displacements of a large number of individual cells. This is done by means of a random-walk procedure (OLLINGER 1998). The assumption that the vertical distribution of a passive tracer can be described solely in terms of a turbulent exchange parametrization may not be valid if largescale convection (especially in autumn) also contributes to the vertical transports. The time scales of small-scale turbulent diffusion and large-scale vertical convection are known to differ (IVEY & IMBERGER 1991). Consequently, the light history of an algal cell transported by convection will differ from that of an algal cell transported by turbulent diffusion. However, as vertical convection mainly occurs in autumn or during clear nights, the use of our approach appears to be justified for the present purpose. Although we know that plankton does not necessarily behave like a passive tracer (MACINTYRE 1993), we ignore this aspect since it is not feasible to incorporate the species-specific variations into the model.

In order to quantify the losses imposed by vertical mixing on autotrophic plankton, three distinct water layers were defined ranging from the depths of 0-8, 8-20, and 20-100 m. This vertical subdivision follows the biological sampling scheme and mostly biological reasoning. For example, algal growth in Lake Constance is often not light-limited within the uppermost 8 m, whereas a positive net photosynthesis is hardly found below 20 m (HÄSE et al.1998). To condense the results of our hydrodynamical model concerning vertical eddy diffusivity, we defined so-called exchange rates, p_{ij}, which indicate the fraction of a passive tracer which is transferred per day from a layer between z_i and $z_i + \Delta z_i$ to another layer between z_j and $z_j + \Delta z_j$, where z_k is the top level of the k^{th} layer and Δz_k its thickness. At our sampling site and for the above mentioned reasons, we take an uppermost layer ($z_1 = 0$, $\Delta z_1 = 8$ m), an intermediate one ($z = 8$ m, $\Delta z_2 = 12$ m), and a deep stratum ($z_3 = 20$ m, $\Delta z = 80$ m). According to expectations, the exchange rates are determined by the power of the density stratification to prevent wind-induced turbulence to be dispersed towards greater depths (ÖLLINGER & BÄUERLE 1998). Generally, exchange rates are small at low wind speeds, but it should be mentioned that turbulent kinetic energy remains in the lake for several hours after the cessation of previous wind events. Among others, the present study extends the previous work on potential relationships between p_{ij} and algal standing stocks (GAEDKE et al. 1998b) by including more years of investigation and by providing an alternative, more comprehensive measure of the downward mixing of plankton by computing daily residence rates, R_h (in the following, we take h = 20 m). R_h is defined as the fraction of particles remaining at the end of a day in the same stratum into which they were placed at its beginning. R_{20}, e.g., is tightly related to p_{12} and p_{13} by

$$R_{20} = 1 - (p_{13} * V_1 + p_{23} * V_2)/(V_1 + V_2),$$

where V_1 and V_2 represent the respective volumes of the uppermost (0-8 m) and intermediate (8-20 m) water layers. The fraction of an ensemble of photosynthesizing cells resting in the uppermost 20 m before being dispersed by turbulent diffusion into the lower, dark part of the water column should be an adequate measure of the capability to harvest light. Provided solar radiation is favourable, consecutive days with high values of R_{20} imply on the one hand the potential for strong algal growth and, on the other hand, the development of a pronounced density stratification.

Results

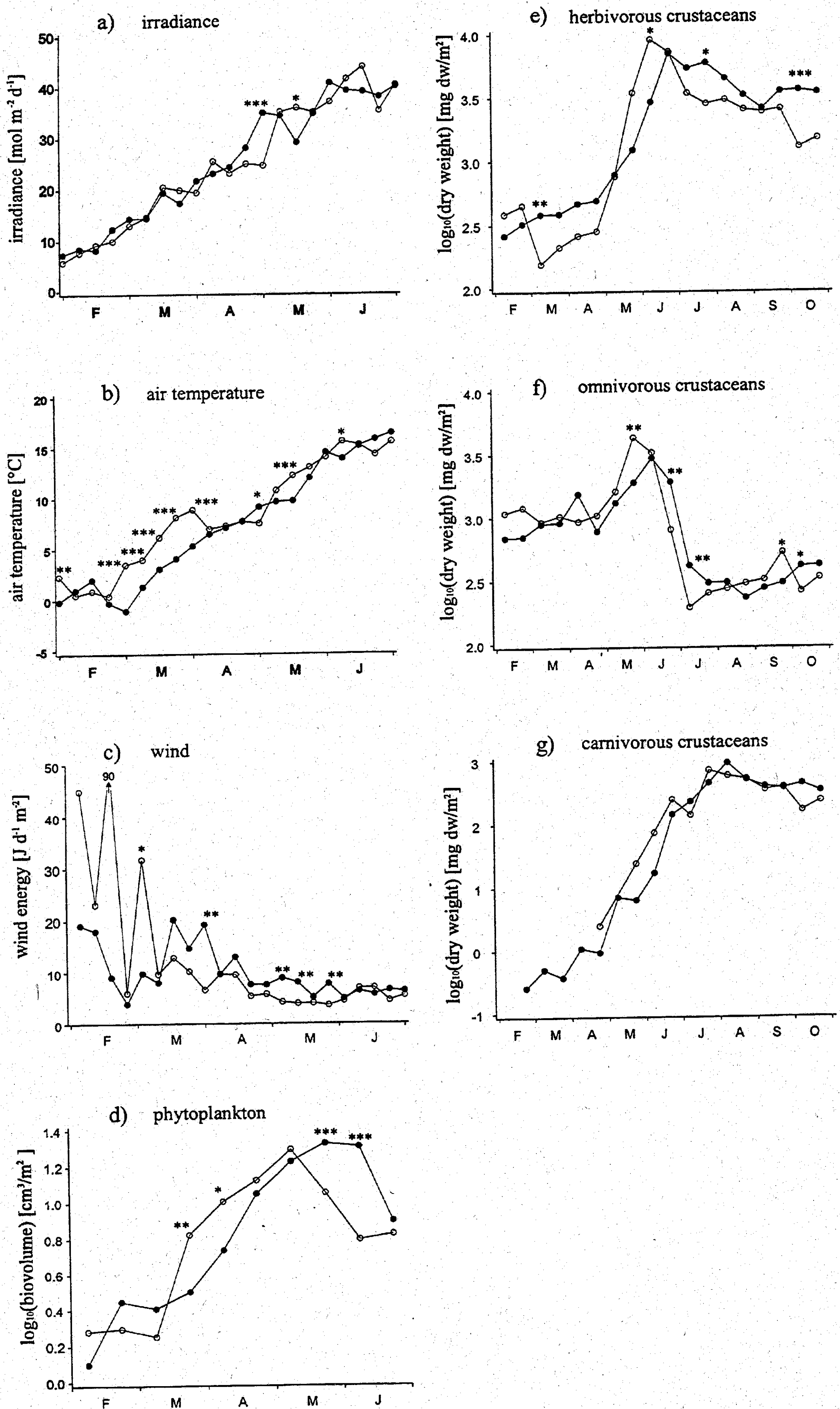
Potential relationships between meteorological parameters and changes of algal standing stocks in spring evaluated from long-term measurements

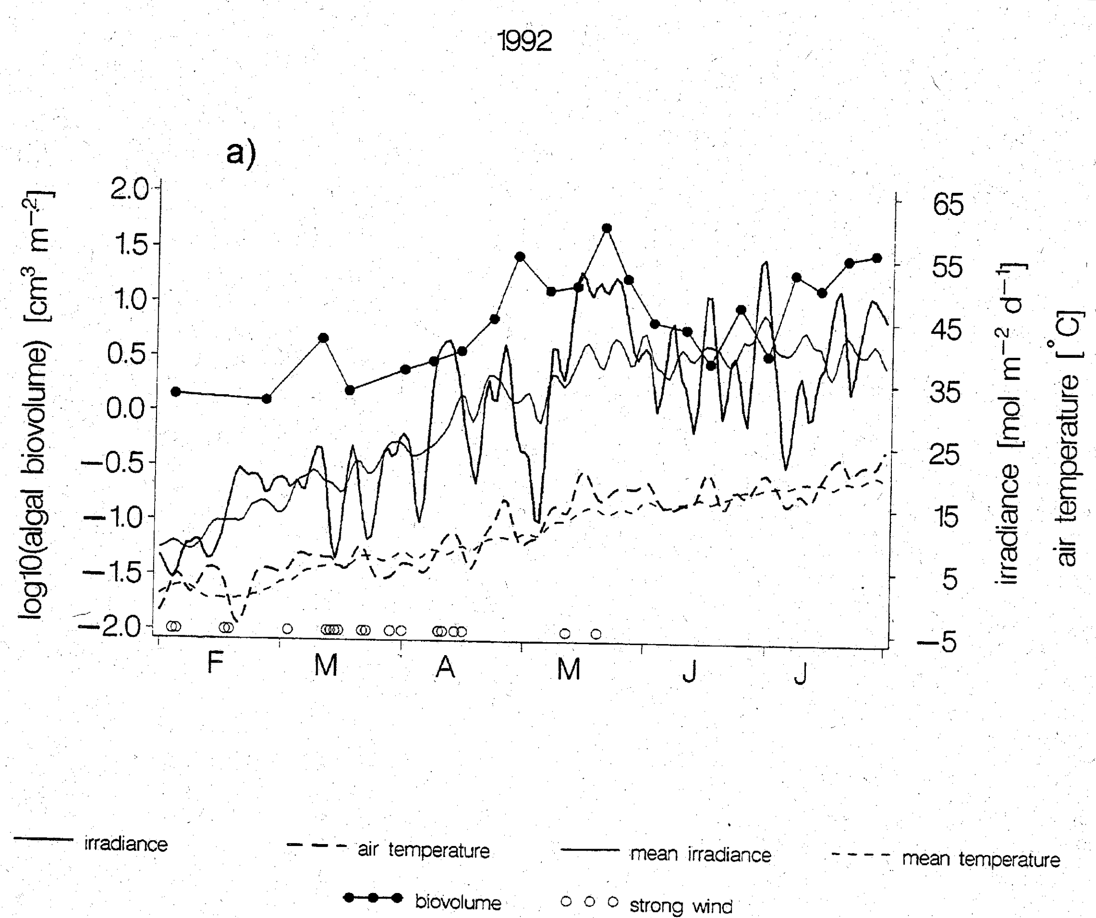
Based on measurements of algal biovolume, chlorophyll concentrations, and Secchi depth, the years 1979-94 were grouped into two classes according to the calendaric date of the first pronounced net increase of algal biomass. Class I represented the years with an early enhancement of phytoplankton biomass (1989-91, 1993-94), and class II the others (1979-88, 1992). During class-I years, surface irradiance was at or below the long-term average (Fig. 1a), whereas air temperature around March was significantly higher (Fig. 1b). The differences in air temperature between the two classes amounted to 3.6 °C during this time. No systematic differences in wind speed (for exact computation see method section) were found between class-I and class-II years during February, March, or April (Fig. 1c). In May, an almost consecutive period of relatively strong average wind occurred during class-II years, but its direct relevance for algal growth has to be questioned since stratification was already fairly stable at this time of the year (see below). Considering daily wind energy during individual years, again no systematic differences between the two classes of years were found. Algal biomass differed significantly between the two classes in late March and early April (class-I years higher), and in late May and early June (class-I years lower) (Fig. 1d). This delivers a first indication for a temporal shift in vernal algal growth and decline depending on air temperature.

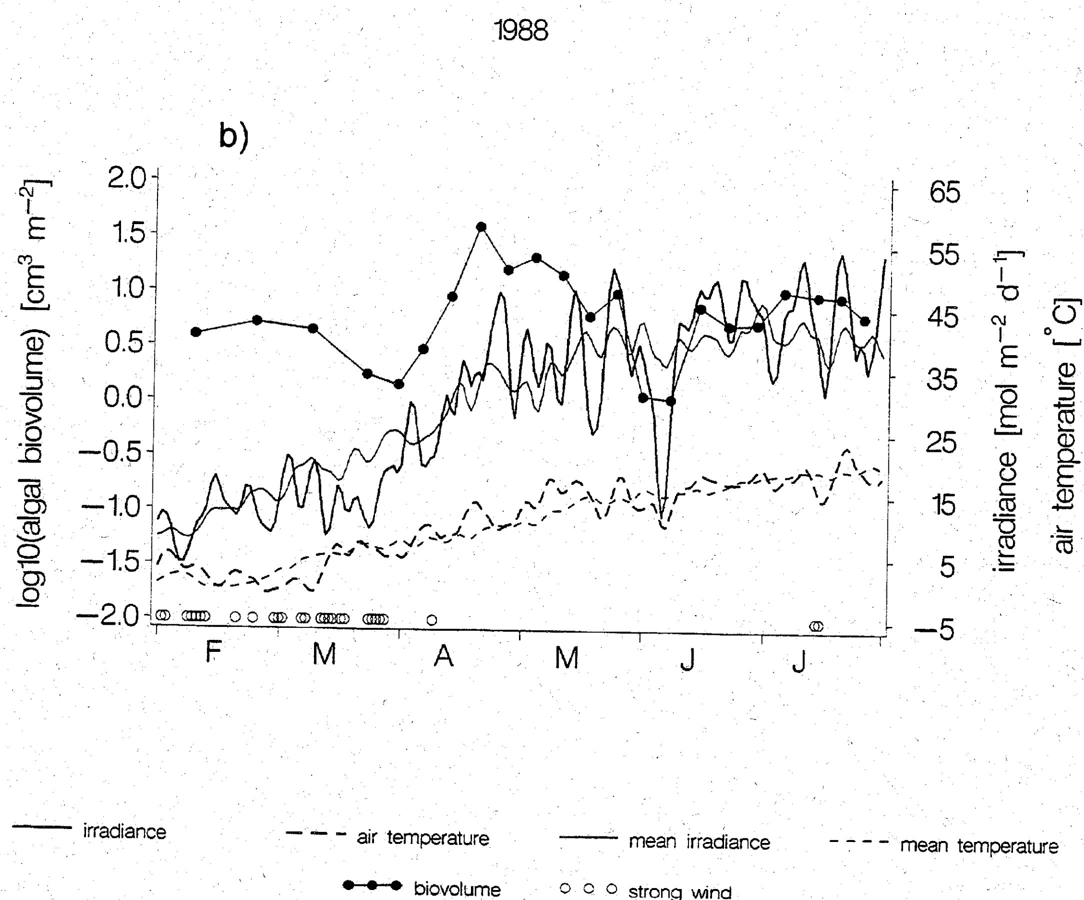
During individual years, irradiance and algal biomass covaried often only weakly in spring (Fig. 2) which demonstrates that daily surface irradiance alone has merely a restricted predictive power for algal growth conditions. A similar result was obtained when considering air temperature exclusively, and when using chlorophyll concentrations rather than algal biovolume as a measure for algal standing stock. Except for a few individual sampling dates, algal biovolume and chlorophyll concentration covaried closely in spring (GAEDKE et al. 1998b, GAEDKE 1998b). Regarding air temperature and surface irradiance simultaneously reduced the unexplained variability to some extent. Pronounced wind events often coincided with constant or decreasing algal standing stocks, but occasionally an overall positive net population increase was observed despite individual incidents with high wind energy (e.g. April 1992, Fig. 2a). Inspecting the meteorological conditions for each period with a change of algal standing stock during all years of investigations is already tedious for two parameters if done by hand, and is only feasible for three (i.e., including the effect of wind) for selected episodes, two of which will be subsequently considered.

For example, spring 1992 was characterized by an exceptionally early, preliminary increase of algal biomass in late February and early March which points to unusual weather conditions (Fig. 2a). In mid February 1992, very low air temperature, average irradiance, and several days of strong wind prevailed. After that, temperature and irradiance augmented above the long-term average and wind speeds were exceptionally low (the single day with strong wind shown in Fig. 2a was just above the threshold of 5 m/s), i.e., all meteorological factors favoured simultaneously low vertical mixing rates and, thus, spring algal growth for about two consecutive weeks. Algal standing stocks responded to this rare episode although temperature and irradiance were still considerably lower than in April when most blooms happen (Fig. 2, cf. Fig. 6). Algal

Fig. 1. Comparison of weather conditions and of phyto- and zooplankton spring development between years with an early (1989-91, 1993-94) (open circles) and later (1979-88, 1992) (full dots) onset of algal spring growth. a) irradiance (weekly averages of daily mean photosynthetic active radiation), b) air temperature (weekly averages of daily measurements), c) wind speed (weekly averages of hourly measurements, for details see text), d) phytoplankton biovolume (biweekly averages of weekly or biweekly measurements on a logarithmic scale), e) herbivorous crustaceans (daphnids, *Bosmina, Eudiaptomus*), f) omnivorous crustaceans (cyclopoid copepods), g) carnivorous crustaceans (*Leptodora, Bythotrephes*) (all biweekly averages of weekly or biweekly measurements on a logarithmic scale). The x-axis covers February to June for the meteorological parameters and phytoplankton (season responder) and February to October for the crustaceans (season anticipators) to account for the different response times of the differently sized organisms. Significant differences between early and late years are indicated by * (5-% level), ** (1 -% level), and *** (0.1-% level).


a) irradiance
irradiance [mol m-2 d-1]
0 10 20 30 40 50
F M A M J
b) air temperature
air temperature [°C]
-5 0 5 10 15 20
F M A M J
c) wind
wind energy [J d-1 m-2]
0 10 20 30 40 50
90
F M A M J
d) phytoplankton
log10(biovolume) [cm3/m2]
0.0 0.2 0.4 0.6 0.8 1.0 1.2 1.4
F M A M J
e) herbivorous crustaceans
log10(dry weight) [mg dw/m2]
2.0 2.5 3.0 3.5 4.0
F M A M J J A S O
f) omnivorous crustaceans
log10(dry weight) [mg dw/m2]
2.0 2.5 3.0 3.5 4.0
F M A M J J A S O
g) carnivorous crustaceans
log10(dry weight) [mg dw/m2]
-1 0 1 2 3
F M A M J J A S O


1992
a)
log10(algal biovolume) [cm³ m⁻²]
2.0
1.5
1.0
0.5
0.0
−0.5
−1.0
−1.5
−2.0
65
55
45
35
25
15
5
−5
irradiance [mol m⁻² d⁻¹]
air temperature [°C]
F
M
A
M
J
J
irradiance
air temperature
mean irradiance
mean temperature
biovolume
strong wind


1988
b)
log10(algal biovolume) [cm³ m⁻²]
2.0
1.5
1.0
0.5
0.0
−0.5
−1.0
−1.5
−2.0
65
55
45
35
25
15
5
−5
irradiance [mol m⁻² d⁻¹]
air temperature [°C]
F
M
A
M
J
J
irradiance
air temperature
mean irradiance
mean temperature
biovolume
strong wind

biovolume increased threefold (Fig. 2a), chlorophyll concentrations eightfold (cf. Fig. 6f; HÄSE et al. 1998), and Secchi depth decreased from 14 to 6 m. In mid March, three pronounced wind events each lasting several days occurred, and light and temperature were often below and rarely above the average. Typical winter data of algal biovolume, chlorophyll concentration, and Secchi depth indicated the termination of the first algal bloom, and a period followed with little increase of algal standing stocks until mid April. Subsequently, all meteorological parameters were within the range of the long-term average which was sufficient at that time of the year for a second and more pronounced algal development. Peak values were reached in May when consistently high temperatures and irradiances occurred in the absence of strong wind. The decline of algal biovolume and chlorophyll concentrations around late May or June which gave rise to a clear-water phase is primarily attributable to strong grazing by daphnids rather than vertical mixing (e.g. SOMMER 1987).

Another occasion where increments of algal standing stock could be related directly to ambient meteorological parameters by hand took place in March and April 1988 owing to a marked change from relatively long-lasting adverse to favourable weather conditions (Fig. 2b). In March 1988, very low irradiance, a frequent occurrence of strong wind, and air temperatures close to the long-term average were observed, whereas from early April onwards relatively high air temperatures and later high irradiance also prevailed. The wind speed was continuously around the long-term average. These weather conditions resulted in an immediate outburst of algal standing stocks. Chlorophyll concentrations rose by a factor of 20 within 2 weeks (Fig. 2b, cf. Fig. 6). A comparable increase was found only in 1987, a year which was likewise characterized by a strongly retarded spring development. To conclude, the onset of phytoplankton development can be linked to the ambient meteorological conditions if the relevant parameters largely covary in such a way that they either exert all positive or all negative effects on water column stability. However, such situations are not the rule, but the exception for Lake Constance (GAEDKE et al. 1998a). Otherwise, a mathematical tool is required to quantify the complex interplay of the direct and indirect effects of the various meteorological factors on the mean light intensity to which individual algae were exposed (see below).

Potential relationships between meteorological parameters and population dynamics of crustaceans evaluated from long-term measurements

In contrast to phytoplankton, high air temperatures in March/April as found during class-I years did not translate immediately into high biomasses of crustacean zooplankton during these months (Figs. 1e, 1f). In May, however, significantly higher biomasses of herbivorous crustaceans and cyclopoid copepods were recorded during class-I years. One reason for this time lag in reaction may be the longer generation times of crustaceans compared to algae. Herbivorous crustaceans built up two to three times more biomass in May and obtained

Fig. 2. Comparison between the spring development of daily irradiance (moving-average over 5 days, full thin line), air-temperature (moving-average over 5 days, broken line underneath), strong wind events (i.e., average daily wind speeds above 5 m/s, indicated at the bottom), and algal biovolume (full thick line, individual observations marked with full dots, please note the logarithmic scale) during spring a) 1992 and b) 1988. The strong reduction of algal biovolume around June represents the clear-water phase caused by intense grazing largely independent of weather conditions.

maximum biomasses earlier during class-I than during class-II years. In contrast, from July onwards, biomass of herbivorous crustaceans in class-I years was consistently lower than in class-II years. Hence, a classification of years based on the date of the onset of the first vernal phytoplankton bloom separated years with high and low biomasses of herbivorous crustaceans in summer. A similar shift in the biomass development was observed for cyclopoid copepods (Fig. 1f). Class-I years exhibited higher cyclopoid copepod biomasses in May and lower ones in June. Biomass of carnivorous crustaceans did not differ significantly between class-I and -II years (Fig. 1g).

The biomass increase of herbivorous crustaceans was due mainly to an increment in daphnid populations. The biomass of *Eudiaptomus* oscillated far less and that of *Bosmina* was more than one order of magnitude smaller compared to daphnids (STRAILE & GELLER 1998). The biomass increase of daphnids closely followed the spring water temperature during all years of investigation (for examples see Fig. 3). During 1987 (a class-II year), it took until mid June until the water temperature in the depth of 4 m exceeded 12 °C and daphnid biomass achieved values exceeding 1 g DW/m². In contrast, both thresholds were reached already in mid May of 1988 and 1992 (class-II years) as well as of 1990 (a class-I year). This suggests that daphnid growth is strongly linked to spring temperatures, but not to the onset of the spring algal development.

Potential relationships between meteorological parameters, turbulent vertical exchange coefficients, and daily residence rates inferred from a hydrodynamic model

In Lake Constance, water column stability varied as expected greatly throughout the season and with depth, which will be illustrated by observations from the first half of 1994 (Fig. 4). Comparing the temporal variations of the irradiance, wind speed, turbulent vertical exchange coefficient (eddy viscosity), and daily residence rate for the upper 20 m, R_{20}, revealed a strong impact of meteorological conditions and especially of wind speed on vertical mixing rates. For example, the depressions in R_{20} from day 70 to 85 and from day 90 to 105 can be traced back to moderate and strong winds which prevented the development of a persistent stratification. After day 110, when winds stayed faint and irradiance intensified again after a week with extremely low values, turbulence was restricted to the near surface region of the water column and R_{20} switched to maximum values. Although in May and June moderate winds were still able to cause some short downward mixing events, both eddy viscosity and R_{20} indicated that day 110 is the beginning of stable stratification in 1994 (Fig. 4). These findings are representative for all other years of investigations.

The strong and direct impact of meteorological factors on vertical mixing during the colder part of the season implies that mixing varied pronouncedly between years (Fig. 5). Consistently high values of R_{20} were found from about May to October. During other times, R_{20} fluctuated widely or was very low for longer periods of time suggesting that a large proportion of the planktonic populations were lost from the euphotic layer each day. Within spring months, interannual and short-term variability of R_{20} was highest, consecutive high values of R_{20} were restricted to a few weeks at most, and R_{20} responded sensitively to weather conditions including individual wind events (see below). At the end of the year, R_{20} decreased to values around 0.20. This is merely due to the ratio between the volume above the reference depth (20 m) and the total volume of our model lake. It reflects the fact that in the absence of

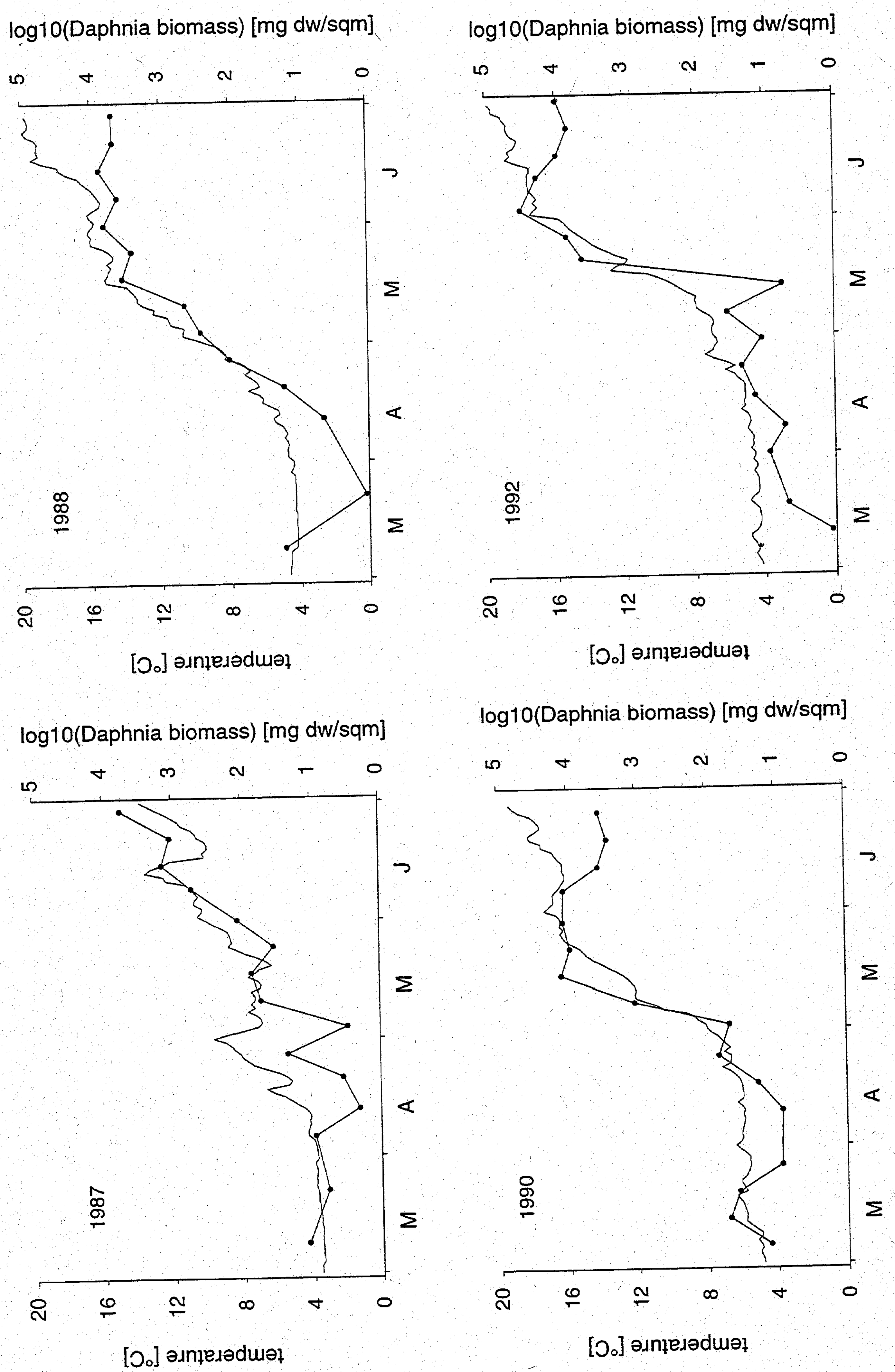


Fig. 3. Spring development of daphnia biomass (full dots) and water temperatures at the depth of 4 m (thin line) during representative years.

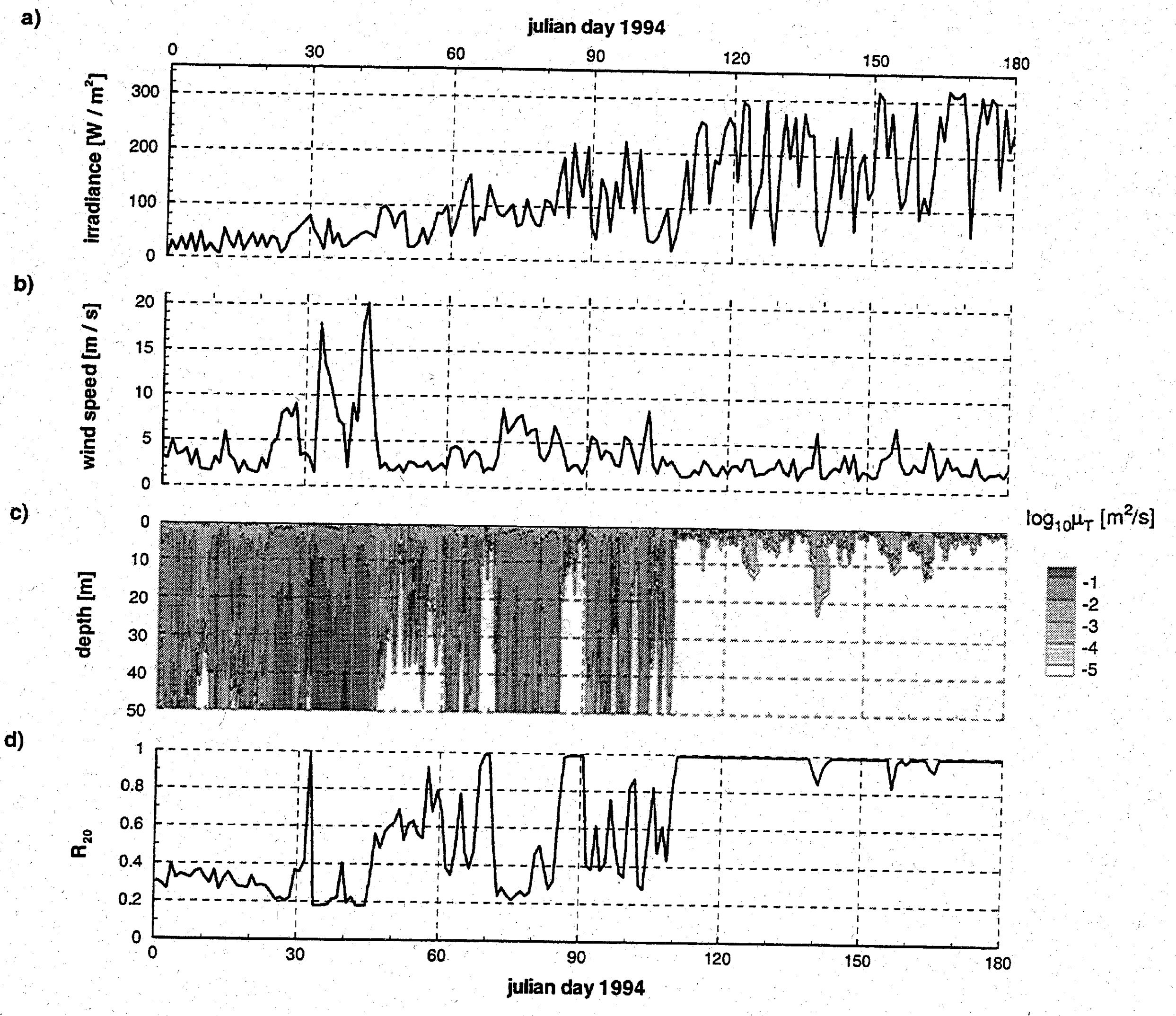


Fig. 4. The turbulent state of the water column of Upper Lake Constance modelled by a hydrodynamic model for the first 180 days of 1994. a) irradiance, b) wind speed, c) turbulent vertical exchange coefficient, μ_T, in the uppermost 50 m, and d) daily residence rate for the upper 20 m, R_{20} (see text for detailed explanations).

stratification the tracer is mixed throughout the whole water column and particles may leave and reenter the uppermost stratum within one day. Hence, the relapses of R_{20} to values of about 0.20 which may occur in March and April have to be interpreted as breakdowns of a weak, transitory stratification. Likewise, higher values of R_{20} occasionally derived for late February and early March indicate that planktonic particles may already remain within the upper 20 m for a fair number of consecutive days in late winter. The situation during winter 1987 was unique owing to an inverse stratification during January and February.

Potential relationships between daily residence rates and changes of phytoplankton standing stock

The large responsiveness of water column stability and residence rates to previous and ambient meteorological parameters provides a key to the understanding of the impact of weather

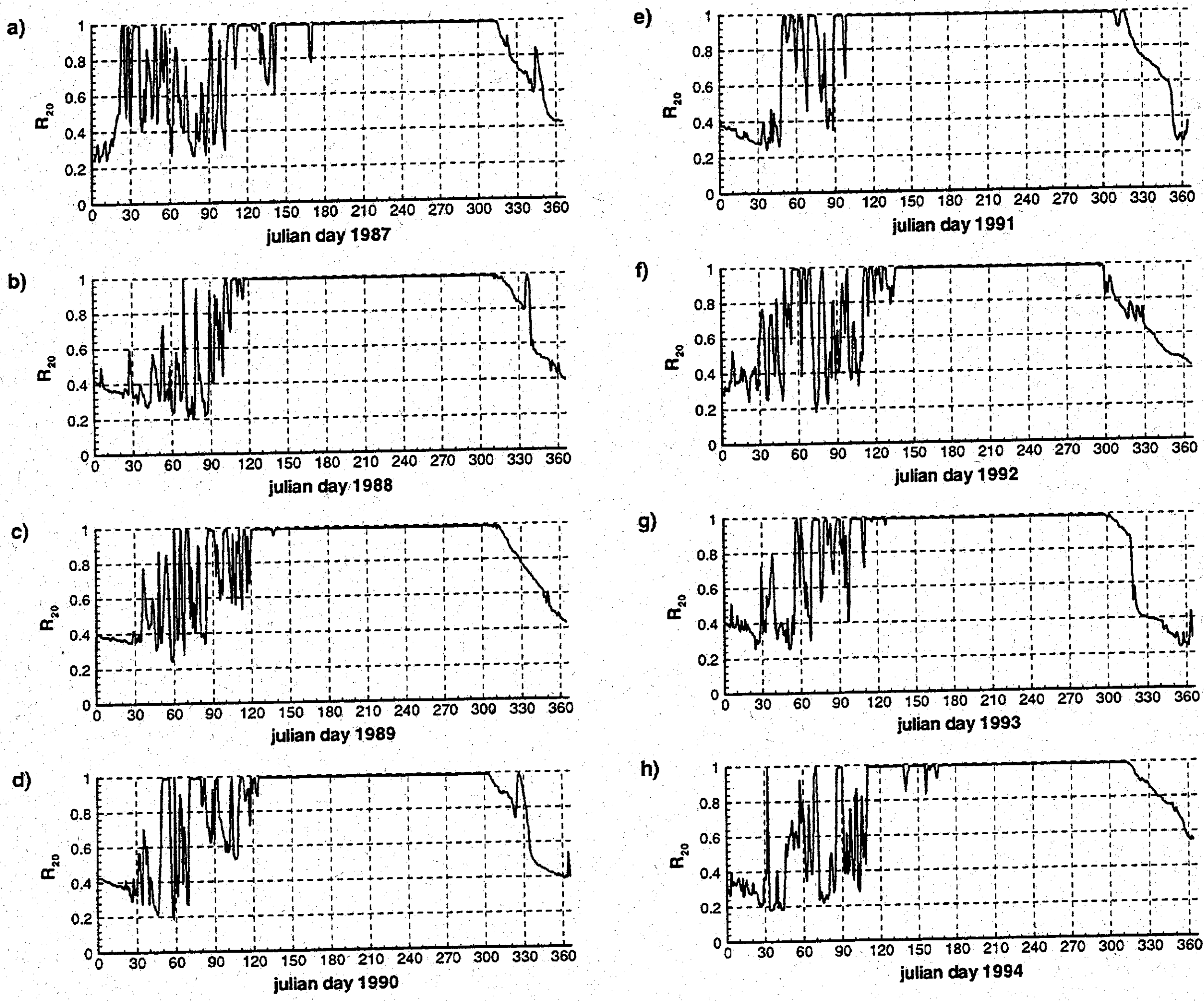


Fig. 5. Annual dynamics of daily residence rates for the upper 20 m, R_{20}, in 1987-94.

conditions on plankton development, especially in spring. A comparison of the temporal variation of R_{20} with that of algal biomass revealed a tight relationship between the two parameters (Fig. 6). Hardly any significant enhancement in algal standing stocks was found when values of R_{20} were low. Vice versa, high values of R_{20} for a consecutive period of time indicating that planktonic cells were safe from being mixed from the upper 20 m to greater depth (i.e. below the euphotic zone) consistently gave rise to an immediate increase of algal biomass. This clearly shows that light conditions limited growth. Considering the covariation of R_{20} and algal biomass during individual years, 1987 and to a lesser extent 1988 were characterized by low values of R_{20} throughout March and the beginning of April which coincided with a lack of early increases of algal biomass. After the sudden stabilization of the water column in mid April, an exceptionally rapid increase of algal biomass immediately followed (see above, Fig. 2). It also yielded very high maximum chlorophyll concentrations (HÄSE et al. 1998), presumably owing to the absence of grazers which could not track the changes of growth conditions so quickly. The decrease of chlorophyll concentrations after day 110 was not attributable to physical processes, but to intensifying grazing pressure exerted mostly by daphnids (clear-water phase). Spring 1989 was marked by frequent and pronounced variations of R_{20},

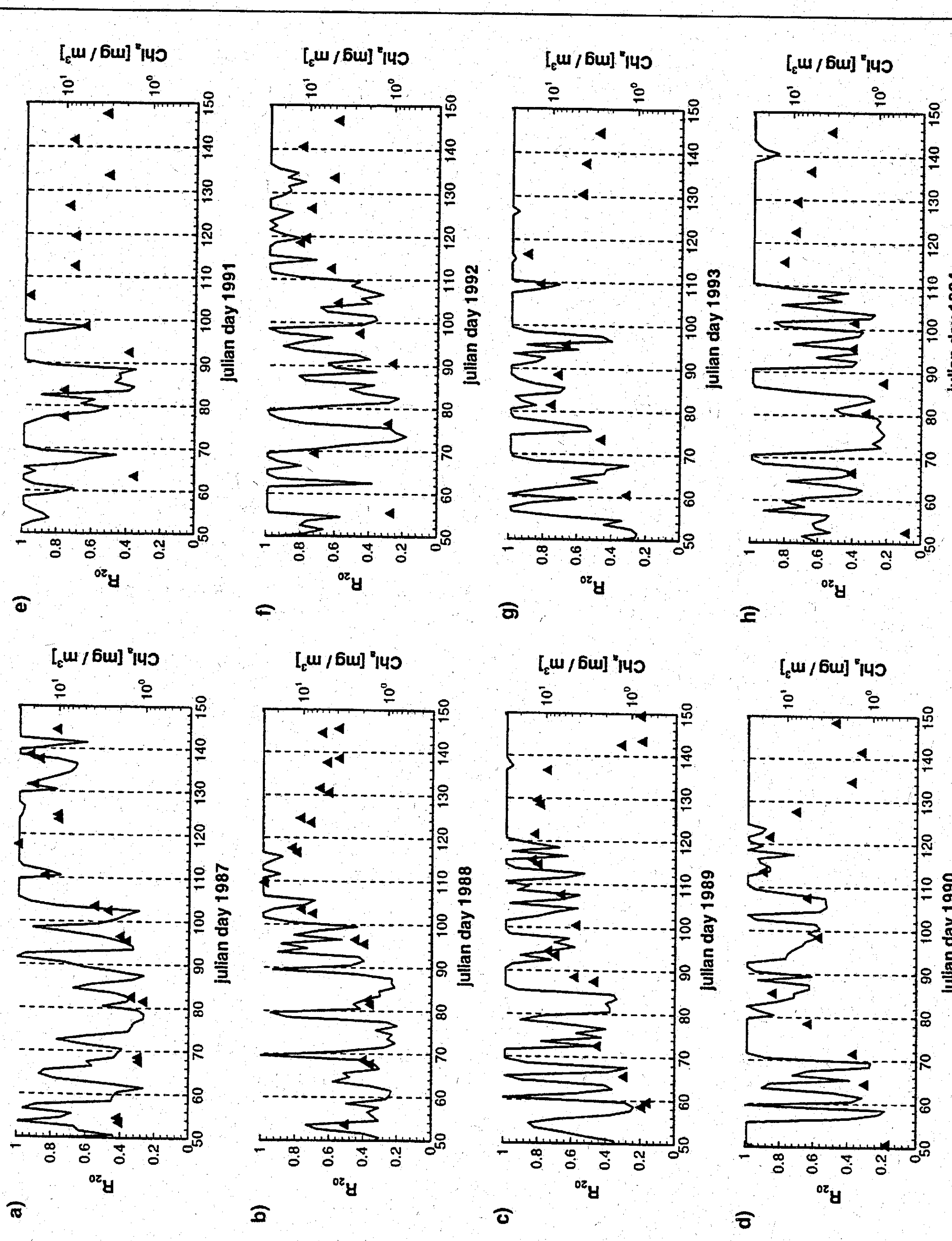


Fig. 6. Comparison between daily residence rates for the upper 20 m, R_{20}, and spring algal development indicated by chlorophyll concentrations measured in the uppermost 20 m in 1987-94.

evidencing that growth conditions of phytoplankton varied greatly within a few days (Fig. 6c). Despite having 12 observations of chlorophyll concentrations in March and April, the temporal resolution of measurements was too low to allow for such variability. The low chlorophyll concentrations in late May feature the grazing-induced clear-water phase. In 1990, in accordance to high values of R_{20}, chlorophyll concentrations augmented from about the 10^{th} of March onwards. The rather high chlorophyll concentration at day 85 may either indicate that algal growth was little affected by a daily loss rate of 10-30%, owing to mixing which prevailed during the previous days (Fig. 6d), or that chlorophyll concentrations increased very pronouncedly prior to the reduction of R_{20} which subsequently caused a moderate decline of chlorophyll concentrations. The following low levels of chlorophyll at day 98 and 107 coincided with low values of R_{20}. Relatively poor sampling frequencies in March and early April 1991 prevent more detailed evaluations. Late February and early March 1992 were characterized by comparatively high values of R_{20} to which algal standing stocks clearly responded (see above). During the following period, R_{20} and chlorophyll concentrations were consistently low, and the major development was retarded till late April, presumably due to considerable losses by vertical mixing. The years 1993 and 1994 confirmed the findings described above (Fig. 6).

To summarize, during most years of investigation, algal biomass started to rise by the end of March in Upper Lake Constance, but this trend was often subsequently interrupted or reversed by adverse conditions during the following weeks. Preliminary net increases of algal biomass did appear as early as late February and early March under exceptionally favourable circumstances, but were rapidly terminated by changes of weather conditions (e.g. 1992). A delay of any vernal development until mid April occurred only under exceptionally unfavourable meteorological conditions (e.g. 1987). From May onwards, phytoplankton dynamics were much less responsive to short-term fluctuations of the weather situation during all years of investigations.

Potential effects of alternative scenarios of weather conditions on vernal algal development

The hydrodynamic model may be used to explore the effects of alternative weather conditions on the extent of vertical mixing. We simulated the development of water column stability in spring 1992 with the observed wind speed, and with half of the recorded values. All other meteorological parameters were kept identical. Values of R_{20} calculated with the actual wind speed were already high in late February and early March. The following low data computed for the period from mid March to mid April indicate that, on average, more than half of the particles residing within the upper 20 m at the beginning of the day were mixed to depths greater than 20 m within that day (Fig. 7). These findings are in accordance with measurements of algal biomass showing an increase in late February/early March 1992, lower values in mid March, and a prominent rise from late April onwards (Figs. 2, 6). The hydrodynamic model suggests that strong winds in mid March of 1992 disturbed algal growth and, together with average meteorological conditions in April, retarded the main algal development till May, but sampling intervals were too large to analyse the potential consequences of each peak and trough of R_{20} (cf. Figs. 2, 7).

The corresponding calculations of R_{20} based on wind speeds reduced to 50% of the observed ones revealed that under such conditions stable stratification would have been reached by the end of March (Fig. 7). This suggests that the vernal algal development of 1992 would have been significantly different if winds had been more moderate than ascertained. Especially, the main algal peak in mid May would be expected to have occurred several weeks earlier.

Discussion

A comparison of the temporal development of basic meteorological factors and algal standing stocks can be performed based on easily assessable raw data. This approach is easily communicated, reproducible for similar ecosystems which facilitates cross-system comparisons, and does not involve the effort and uncertainties inevitably implied in complex hydrodynamic models. The moderate degree of covariation found between phytoplankton standing stocks and daily irradiance or air temperature in spring refers on the one hand to a direct and/or indirect influence of these parameters on algal population growth. Similar relationships were found in an extended time series of chlorophyll concentrations and diatom abundances in Lake Windermere, pointing to irradiance-dependent phytoplankton dynamics during the vernal blooms (NEALE et al. 1991). On the other hand, the considerable amount of unexplained variance in these covariations suggests that neither irradiance nor air temperature nor wind alone provide reliable indicators of algal growth conditions in spring in Upper Lake Constance. This signifies that the presumably complex synergistic direct and indirect impacts of the meteorological regime on algal biomass in the upper water layer are primarily mediated by water column stability. The latter, in turn, depends in addition to current meteorological factors on the stratification of the water column, and other factors not indicated by ambient meteorological parameters such as the turbulent kinetic energy of shear instabilities from internal seiches which originate from previous wind events.

Another draw back of this method is that its appealing simplicity was achieved at the expense of the capability to understand causal relationships among the numerous potentially influential meteorological parameters. The covariation of daily wind speed, air temperature, and irradiance was low (GAEDKE et al. 1998a). Hence, this approach was supplemented by a comparison of years with an early and later onset of algal growth. It revealed significant differences in air-temperatures between the two classes of years. However, this result should be interpreted with care since it was based on long-term observations rather than on designed experiments. This prevents a systematic study of the relative importance of the individual meteorological factors. Additionally, the allocation of individual years into the two classes was to some extent subjective (e.g. 1992) because, e.g., minor peaks may have occurred prior to the spring development proper which may also be subject to sampling errors. Results were robust against moderate changes of the classification scheme. Considering the years 1987-94, the classification of years according to the timing of the onset of algal growth (Fig. 1) was largely reflected by the values of R_{20} in late February, March, and April (Fig. 6), computed after the allocation of the years into the two classes. A long-term study of small, hypertrophic shallow Lake Heiligensee revealed likewise a significant impact of several consecutive unusually mild winters on the plankton development almost throughout the year (ADRIAN et al. 1995). However, details of the responses and the underlying mechanisms differ greatly between Lake Heiligensee and our deep lake.

The hydrodynamic model provided comprehensive insight into the complex synergistic effects of irradiance, air temperature, wind, and other meteorological factors on water column stability (cf. OLLINGER & BÄUERLE 1998, BÄUERLE & OLLINGER, in prep.). This enables us to

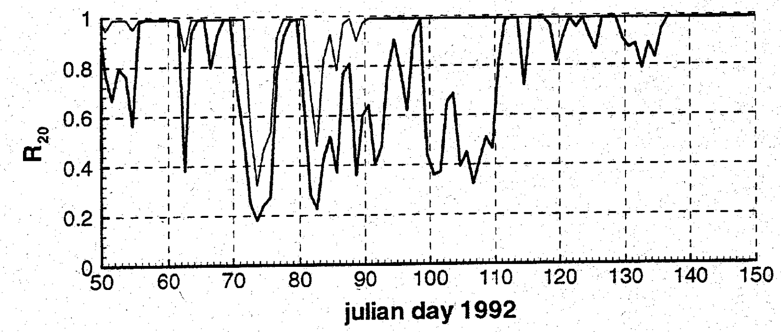


Fig. 7. Water column stability in spring 1992 calculated by the hydrodynamic model with measured meteorological parameters (full drawn line) and with a wind speed reduced to half of the observed value (thin line).

identify which deviations of meteorological conditions from the long-term average at what time of the season are most relevant for vertical mixing. This predictability of vertical mixing based on meteorological parameters, in turn, may allow to forecast roughly the start of vernal algal development under various weather conditions which deviate moderately from those during the period of investigation, given that – as in Lake Constance – a close and consistent relationship between vertical mixing intensity and algal growth exists.

The available temporal resolution of the measurements of algal development imposed a restriction on the validation of all approaches and contributed to the less convincing results obtained by the first one. The sampling frequency varied between twice a week and every 2 (-3) weeks. This is high for long-term records according to current practice, but still rather low for unambiguously recognizing the reaction of the phytoplankton community to a frequently changing weather regime and vertical mixing rates. The latter may have caused a substantial variability of growth conditions and chlorophyll concentrations between two consecutive observations. The data available so far strongly suggest a tight causal link between R_{20} and algal development and never contradict it. However, daily or continuous automated measurements would greatly improve our capacity to validate this hypothesis rigorously. In the present study, the lack of an extremely high temporal resolution in the biological measurements could be compensated partially by the large number of years, as this heightens the chance to detect a potential mismatch between R_{20} and algal development.

In contrast to downward mixing events below 20 m, phytoplankton standing stocks responded much less sensitively to mixing within the uppermost 20 m (GAEDKE et al. 1998b). This finding is in accordance with the idea that in deep lakes significant phytoplankton blooms develop in spring when thermal stratification reduces the vertical mixing depth (e.g., REYNOLDS 1973, HORN & PAUL 1984). Upper Lake Constance has an average depth of 101 m. In winter, Secchi depth and euphotic depth were around 15 and 18-22 m, respectively, and decreased to 5 and 12 m during spring peaks in recent years (TILZER 1984, TILZER & BEESE 1988, HÄSE et al. 1998). Hence, unless the mixing depth is significantly smaller than the depth of the lake, algal biomass is repeatedly redistributed to depths greater than the euphotic zone and accumulation of algae in the euphotic zone is diminished.

In cases where predicting future changes is difficult, current practice is to use scenario analysis. Performing simulations with meteorological parameters somewhat deviating from the observed ones revealed a high sensitivity of water column stability to wind speed in March and April. Similar results were obtained with a previous version of the hydrodynamic model employing vertical exchange rates (p_{13}) (GAEDKE et al. 1998b). An increase of winter air temperatures by 2 °C or the omission of an individual storm event significantly influenced vertical mixing and, thus, presumably algal population growth. The first result is supported by the findings obtained by classifying all years of investigation according to the date of the onset of vernal algal blooms and comparing the meteorological conditions in both classes of years. With respect to current predictions of global climate change, investigations of the lake's response to such alterations in weather conditions may improve our capabilities to predict future changes in lake ecosystems.

In pelagic food webs, body size and trophic positions and, hence, the strength of the direct impact of the light and nutrient regime roughly covary. This implies that crustaceans have longer reaction times to external perturbations than phytoplankton, owing to their larger body size, and that they respond less sensitively, e.g., to vertical mixing owing to a lack of direct dependence on light and nutrient conditions. The present study confirms a slower response of crustaceans which exhibited a remarkable memory of winter weather conditions until summer. Furthermore, the mechanisms by which phytoplankton and crustaceans were apparently influenced by the weather regime differed greatly. The peaks and troughs of algal standing stocks were closely related to the vertical mixing intensity independently of ambient water temperatures, as indicated, e.g., by the early algal development in February 1992 when water temperatures were still very low.

In contrast, population growth rates of daphnids closely covaried with surface water temperature (Fig. 3). In spring, daphnid growth is mostly affected by food supply and temperature which, in turn, both depend on vertical mixing intensity. In principle, three different scenarios may be distinguished on how vertical mixing intensity indirectly influences daphnid growth. (1) High mixing rates imply low surface temperatures and low food concentrations which both oppose a build-up of daphnid biomass. (2) In contrast, when low mixing rates occur together with elevated surface temperatures and, consequently, relatively high algal abundance as found, e.g. in 1988, growth conditions for daphnids are favourable both in respect to food and temperature. (3) Situations in which not just mixing rates, but also water temperature and vertical temperature gradients are low, as found in February/March 1992, enable us to distinguish between a promotion of daphnid growth by temperature or food. Under these circumstances, algal biomass is rather high, but temperatures are low. Observations during spring 1992 and other years showed that an increase of algal biomass was not sufficient to cause the onset of daphnid population growth. Hence, an increase of water temperature beyond 5-6 °C appears as a prerequisite for substantial spring daphnid growth. The opposite situation where temperature augments without a simultaneous enhancement of water column stability does not occur in deep lakes such as Upper Lake Constance. This implies that algal growth will always start prior to or in parallel with daphnid population growth, which makes food limitation of daphnids very unlikely in spring.

The present study reflects our insight into the impact of weather conditions on the dynamics of pelagic food webs. It already enables predictions of the development and breakdown of vernal algal biomass. Further steps undertaken towards a still better understanding of these processes include intensive analyses with daily sampling and the implementation of automated measurement devices for pigment concentrations as well as a coupling of a hydrodynamical and a biological model which simulates algal development at least during spring (Bäuerle & Ollinger, in prep.). Furthermore, the influence of hydrodynamic conditions on taxonomical and functional properties of the phytoplankton community (Stüber & Gaedke, in prep.) and of the causal links between winter weather conditions, spring water temperatures, and crustacean development in spring and summer (Straile, in prep.) are under study.

To conclude, comparisons of the temporal variations in meteorological parameters and those in algal standing stock helped relatively little to understand the impact of meteorological factors on vernal algal growth as compared to some other studies (ADRIAN et al. 1995, ADRIAN & DENEKE 1996, NEALE et al. 1991). This was presumably caused by the dependence of algal population growth on water column stability and the turbulent kinetic energy in deep Lake Constance in addition to current meteorological conditions. It demonstrates the advantage of taking an interdisciplinary approach to a problem that has up till now commonly been considered by biologists alone. During spring periods, when the hydrodynamic model predicted pronounced mixing of surface water into deep water layers, no significant increases of algal biomass were observed. Vice versa, spring peaks developed quickly when the model predicted a cessation of deep mixing. This tight coupling between vertical mixing and the onset of algal growth combined with the capability to link meteorological conditions and vertical mixing with a hydrodynamic model allowed the evaluation of the potential impact of slightly modified weather conditions on vernal algal development. In analogy to algae, crustaceans were closely linked to physical conditions in spring. However, they responded at a different temporal scale and by a different mechanism, which gives rise to a more pronounced uncoupling of phytoplankton and crustacean dynamics during some years.

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