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Ecology of the phytoplankton of the River Moselle: effects of disturbances on community structure and diversity

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Abstract

A data set on community composition of the phytoplankton of the River Moselle (France) has been used for testing the 'intermediate disturbance hypothesis' (IDH). After a short presentation of the ecology of the river and of its phytoplankton, the main changes in composition and diversity of the suspended algal assemblage are described. It is emphasized that discharge fluctuations, related to weather changes, play a key role, but that biotic factors such as grazing and parasitism may also influence diversity in 'stable' summer conditions.

Introduction

Lake phytoplankton has been worked extensively, whereas few studies have been devoted to the ecology of river phytoplankton (see Descy, 1987, for a brief review). Large rivers, where suspended algae can develop dense and diverse communities, can be viewed as water bodies characteried by:

- short residence times, which vary with the flow rate, i.e. the river discharge through a given cross-section;
- turbulent mixing all over the year; the water column is typically not stratified, save perhaps at very low discharges;
- an abundant nutrient supply from the watershed and the sediment, so that nutrient depletion is seldom observed;
- a high suspended matter concentration, which reduces the transparency.

There is, however, a large difference of scale of disturbance by turbulent mixing between rivers and lakes, which must be emphasized: the river environment is always more or less disturbed, and never experiences periods of stability as they occur in lakes. According to Reynolds (1984 a, b, 1988 a), the river phytoplankton should be dominated theoretically by 'w' (or 'R') species, able to grow in a strongly disturbed and light-limited environment: it should therefore be similar to the phytoplankton of eutrophic (or mesotrophic) lakes during the major mixing events (spring and autumn circulation), with high availability of nutrients and a steep gradient of light related to the Zm:Zeu ratio.

The theory is consistent with the observations: the phytoplankton of large rivers is generally dominated by diatoms (*Asterionella* and *Stephanodiscus* spp.) during spring and autumn, while green algae (mostly Chlorococcales) and cryptomonads may develop best in summer conditions. Eventually, at very low discharges, a typical succession leading to Cyanobacteria dominance (*Microcystis aeruginosa* Kütz., *Oscillatoria agardhii* Gom., etc.) may be observed.

The river discharge is a major integrating factor related to important processes affecting algal communities (rate of turbulent mixing, nutrient supply from the watershed and the sediment, light regime in the water column *via* the amount of suspended matter). Furthermore, discharge seems to control phytoplankton growth through a 'dilution' process (Descy *et al.*, 1987): in a given river stretch of length x, the 'dilution rate' depends on the reciprocal of the cross-section area (1/A) and the linear lateral inflow (dQ/dx). Suspended algae can build up significant populations only when their net growth rate (taking into account the loss factors) exceeds the dilution rate. This control of algal development by discharge favors further fast-growing and disturbance-tolerant algae (i.e. the 'colonizers' or 'pioneers'), at least in fluctuating conditions.

In the present paper, particular attention is given to the effect of discharge and its variations on the diversity of the phytoplankton of the river Moselle (France). It must be emphasized that the data were not initially collected in order to test the intermediate disturbance hypothesis: the frequency of observations may be too low, so that the assessment of the relationship between diversity and disturbance is hardly based on a quantitative approach, but rather on statements which have not been verified on a quantitative basis. So, the choice of the data set was mainly influenced by the interest of testing IDH on river phytoplankton.

Description of the site studied

The River Moselle, a tributary of the Rhine, is 313 km long and has a catchment area of 15200 km^2. Its mean discharge at Uckange, near the border between France and Germany, is 130 m^3 s^{-1} (extreme values: 35–2700 m^3 s^{-1}). The study site is located in the lower French part of the river, at Koenigsmacher, upstream of the nuclear power plant of Cattenom. With regard to the main physical and chemical variables, this part of the river Moselle can be characterized as follows:

- the concentration of major ions is high (mean conductivity greater than 1300 μS cm^{-1} at 25 °C); in particular, the Cl$^-$ concentration may reach 400 mg l^{-1};
- the nutrient supply is important: the lowest measured concentrations are 0.7 mg l^{-1} NO_3^--N, 0.145 mg l^{-1} PO_4^{3-}-P and 0.6 mg l^{-1} Si;
- the vertical attenuation coefficient is higher than 2.5 m^{-1} during the growth period of the phytoplankton, with a maximum above 3 m^{-1}, so that algal growth is light-limited (maximum GP = 14 g O_2 m^{-2} d^{-1} was in 1986; maximum chlorophyll *a* was 57 μg l^{-1} during the same period); mean depth is about 4 m.

Materials and methods

The data set comprises phytoplankton counts from samples collected between October 1985 and October 1986. The techniques for collecting and treating the samples have been described in Descy & Willems (1991): briefly, unfiltered water samples were fixed with Lugol's iodine and concentrated through a sedimentation procedure, so that the final preparations contained the whole plankton, without any size selection.

The Shannon function, H′ (Shannon & Weaver, 1949 in Pielou, 1975), was calculated from the densities of the phytoplankton components (units ml^{-1}): a unit was a cell, even for colonial and filamentous forms, except for the very small-celled Cyanobacteria. The identification level of the algae was the species or an infraspecific taxon, except in a few cases, such as the small *Stephanodiscus* of the '*hantzschii-group*' (see Descy & Willems, 1991 for more details) or the small Thalassiosiraceae (*Cyclotella pseudostelligera* Hust., *Thalassiosira pseudonana* Hasle & Heimdal), which cannot be identified reliably at the light microscope level, even after proper mounting. Not all the taxa recorded in the taxonomic lists were used for the calculations of diversity, but a selection of algae which can be considered as true plankton (Chlorococcales, centric diatoms and some pennates, Cyanobacteria, Euglenophyceae, Cryptophyceae). Most pennate diatoms were encountered as single specimens or empty frustules and were not taken into account. So, the number of taxa per sample which were actually used for determining the Shannon function was typically between 43 and 79. However, this selection does not exclude changes in diversity due to the input of algal cells from some tributaries where true phytoplankton does develop.

In the plankton samples, presence of zooplankton (mainly rotifers) and fungal parasites (chytrids) was simply noted. The water analytical data were obtained from the 'Laboratoire d'Ecologie', University of Metz, France, and the daily discharge measurements at Uckange in 1986 were kindly supplied by J.-L. Salleron, Agence de Bassin Rhin-Meuse, France.

Results

The number of taxa in the phytoplankton of the river Moselle totals 239; the main components are diatoms, Chlorophyceae (Chlorococcales), Cryptophyceae and Cyanobacteria. With respect to the abundances (Fig. 1), centric diatoms dominated over the whole growth period (mid-March to mid-October in 1986). The maximal density of phytoplankton units is close to 40000 ml^{-1}, but very few taxa developed large populations, e.g. 2 or 3 green algae, 7 centric diatoms (Fig. 2). In particular, *Skeletonema potamos* (Weber) Hasle accounts for as much as 50% of the phytoplankton cells over the whole period of observation. This filamentous diatom has a summer optimum, whereas, in the colder seasons, small *Stephanodiscus* dominate.

The mid-summer phytoplankton consists mainly of large unicells and filamentous or colonial forms: their relative abundance may result from an intense grazing pressure removing smaller algal cells, as many rotifers are present at that time of the year. At the same time, many chytrid vesicles can be seen on the filamentous diatoms: this strongly suggests that parasitism could be partly responsible of the phytoplankton decline in late summer. Further details on the phytoplank-

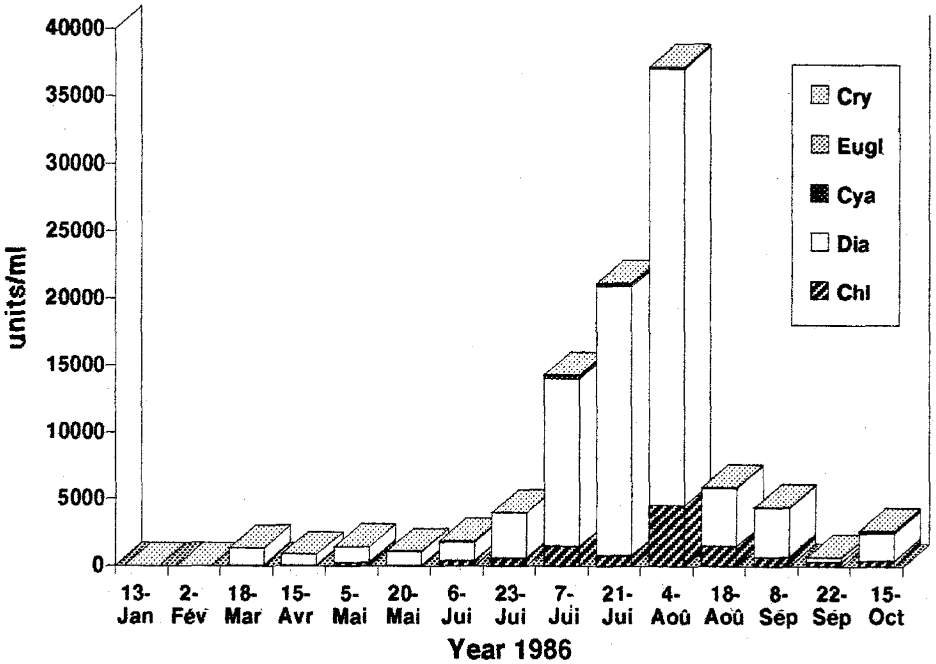

Fig. 1. Changes of the composition of the phytoplankton in the river Moselle at Koenigsmacher in 1986; CHL: Chlorophyceae; DIA: diatoms; CYA: Cyanobacteria; EUGL: Euglenophyceae; CRY: Cryptophyceae.

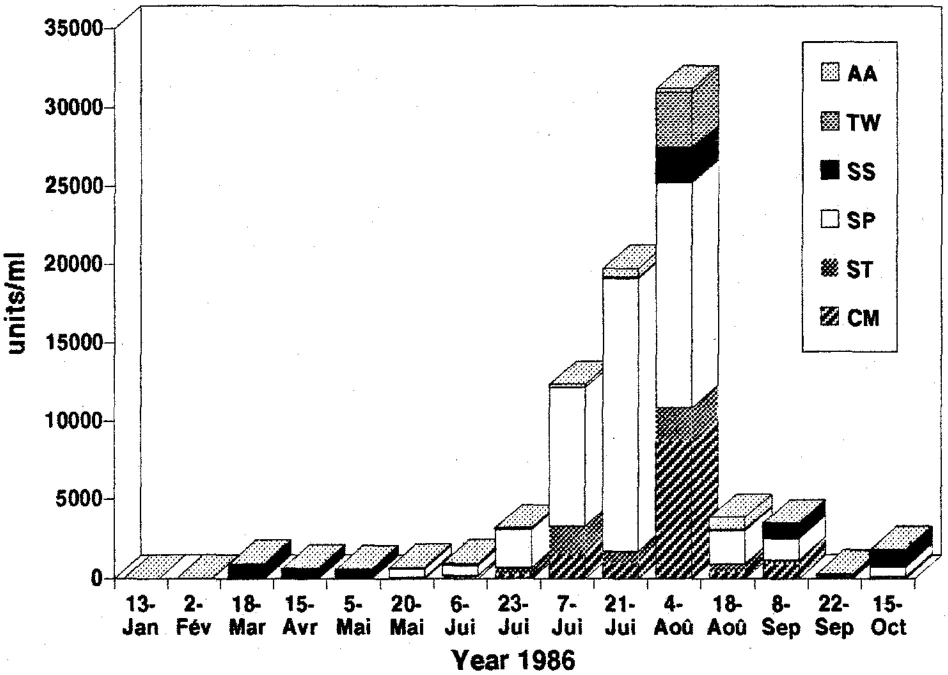

Fig. 2. Seasonal occurrence of some important diatoms in the River Moselle at Koenigsmacher in 1986; CM: *Cyclotella meneghiniana*; ST: small Thalassiosiraceae; SP: *Skeletonema potamos*; SS: small *Stephanodiscus*; TW: *Thalassiosira weissflogii*; AA: *Aulacoseira ambigua*.

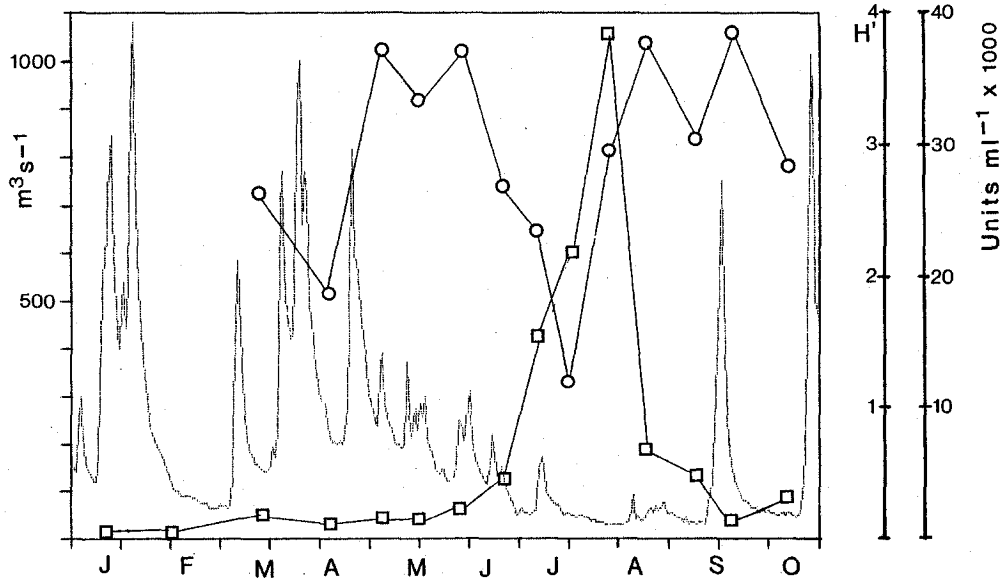

Fig. 3. Variations of the Shannon diversity index (circles) vs. total phytoplankton units (squares) and river discharge (thin line); data from the river Moselle at Koenigsmacher in 1986.

ton of the river Moselle can be found in Descy & Willems (1991).

The seasonal development of the Shannon-diversity is shown in Fig. 3, overlaid on the discharge and the total density of algal units. Four phases can be delimited:

- low diversity in March-April, corresponding to the 'small *Stephanodiscus*' dominance;
- high diversity in May-beginning of June;
- sharp decrease till mid-July, when the *Skeletonema* bloom builds up;
- high diversity values again in August-September, with some fluctuations.

Discussion

The main events in the phytoplankton community changes in the River Moselle can be related to the fluctuations in flow rate and to the biotic interactions. They can be summarized as follows:

- in March–April, which was a period of very large discharge fluctuations, diversity was rather low: the assemblage was dominated by 'small *Stephanodiscus*', able to stand the changing conditions, as well as low temperature and low light;
- in May–beginning of June, diversity increased as discharge decreased and as temperature and light conditions improved; this period of maximal diversity was also characterized by changeable weather, which is reflected by the fluctuations of discharge in the range of 100–400 $m^3 s^{-1}$; the frequency of these changes occured over the time-scale postulated to influence phytoplankton community structure;
- in June–July, discharge decreased and more 'stable' conditions favored a bloom dominated by *Skeletonema*; as a consequence, diversity declined and reached a minimum value;
- in the beginning of August, diversity increased again, as the best growth conditions for most species were met; grazing seemingly contributed to maintain a high diversity, and large unicells and filamentous diatoms developed important populations;
- the late summer and autumn phytoplankton was a low-biomass, but rather diverse community, associated with the *Skeletonema* decline due to parasitism by chytrids; afterward, the weather changes reflected in the discharge peak of September induced some diversity fluctuations: with the return of unstable conditions, a 'small *Stephanodiscus*' assemblage developed again, similar to that of the spring.

Conclusions

As presented above, the changes in the community structure and diversity of the Moselle phytoplankton are clearly connected with the amplitude of weather and discharge fluctuations: in fact, this type of data set is particularly convenient to show changes driven by physical factors, as they operate, apparently, in the absence of nutrient limitation – hence, in the absence of nutrient competition.

The observations tend to verify the three statements of the IDH (Connell, 1978):

- in steady conditions (e.g. the low discharge period in the summer), diversity reaches minimum levels (*Skeletonema potamos* is dominant);
- strong disturbances (high and variable discharge in spring) also induces minimum diversity ('small *Stephanodiscus*' dominance after the discharge peaks);
- a maximum diversity occurs when the disturbances (discharge and weather fluctuations) are in an intermediate range of intensity and frequency (phytoplankton assemblage of May–June).

In other words, large discharge variations clearly result in low diversity and biomass of the potamoplankton, whereas frequent and low-amplitude fluctuations of flow rate favour higher diversity, while biomass remains low, as the algal growth rate barely exceeds the dilution rate (Fig. 3, late spring situation). At this time, the periodicity of the discharge variations is in the range of several days: this is, in agreement with Reynolds (1988 b), a typical situation where allogenic changes interfere with the internal, autogenic processes leading to a 'stable' community dominated by one or few taxa.

However, these conclusions are merely statements, which should be verified by establishing quantitative relations between diversity and measurements of rate and amplitude of change of the physical environment (flow rate, light, turbulence, etc.). Unfortunately, such a quantitative analysis was not feasible with the data available.

In addition, the effect of loss factors of biotic origin (grazing and parasitism) could also be regarded as disturbances able to generate or to maintain a rather high diversity. Indeed, when dealing with the disturbance-diversity concept, disturbances are defined as 'non-biotic and stochastic events that result in distinct and abrupt changes in composition and which interferes with internally-driven progress toward ecological equilibrium' (Reynolds *et al.*, 1993). However, a selective biotic loss process affecting one or more dominant species can result in a higher diversity value, as far as H' is taken as a measurement of diversity. In the river Moselle, such biotic interactions seem to play a significant role when the system has reached some physical constancy.

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