Hydrobiologia **289**: 43–55, 1994.
J.-P. Descy, C. S. Reynolds & J. Padisák (eds), Phytoplankton in Turbid Environments: Rivers and Shallow Lakes.

An elementary, structural analysis of river phytoplankton

C. Rojo[1], M. Alvarez Cobelas[2] & M. Arauzo[2]
[1]*Dept. Microbiología, Univ. Valencia, Burjassot, E-46100 Valencia, Spain;*
[2]*Centro de Ciencias Medioambientales (CSIC), Serrano 115 dpdo., E-28006 Madrid, Spain*

Key words: river phytoplankton, structure, species richness, biomass, diversity

Summary

A structural analysis of river phytoplankton has been carried out based upon published studies on 67 rivers. When available on a yearly basis to account for seasonal variability, five structural features have been chosen: species composition, species richness, species dominance, diversity and biomass (total and per taxonomic groups). Despite the high number of reported studies, most of them cover only some of the aforementioned features. As a result of the low amount of studies, tropical rivers are underepresented. No size distribution studies have been carried out on river phytoplankton. The average species richness amounts to 126, being higher in temperate rivers. Roughly one half of each flora is comprised of sporadic species. No statistically significant relationship between species richness and latitude has been found despite the fact that tropical rivers appear to house fewer species than temperate rivers. Also, one half of the support in the floras are either benthic or tychoplanktonic. Diatoms comprise the majority of species numbers in the whole data set but are substituted by desmids in tropical rivers and by green algae when benthic species are not taken into account. There appears to be lower biomass in river phytoplankton than in lakes. Diatoms are also the major taxonomic group comprising total biomass in rivers but they share clearly a lower fraction in tropical rivers. On an average basis, diatoms appear to be more dominant in rivers than in lakes. The time course of diatom dominance occurs close to the summer solstice in tropical rivers whereas is much more lagged in temperate sites. The diversity of river phytoplankton is highly scattered (0.40–4.40 bits ind^{-1}).

Introduction

Phytoplankton community structure in lakes appears to be a reasonably well studied topic (Smith, 1990). The wealth of knowledge on this topic that has been compiled up to date provides a clear picture of phytoplankton organization in lacustrine environments (Reynolds, 1987). Even certain themes that have been almost neglected in the past have now been covered (e.g. maintenance, diversity, Padisák *et al.*, 1993).

Unfortunately, the analogous picture of river phytoplankton is less clear. Throughout the years, there have been many attempts to unravel the features of river phytoplankton (Zacharias, 1898; Kofoid, 1903; Lemmermann, 1907; Rice, 1938; Blum, 1956; Reynolds, 1988) but they still remain elusive. The reason is that most studies are devoted only to the theme of species richness and many do not cover the entire seasonal variability. Therefore, many studies on river phytoplankton appear not to be well-documented from an ecological viewpoint.

We feel it is time to consider river phytoplankton from a unified point of view, which is likely to result in a more comprehensive picture of this interesting community. Our aim here is: (i) to show some general features of the organization of river phytoplankton, and (ii) to suggest a framework for further structural studies on river phytoplankton, which will emerge from the consideration of already published studies on the topic. In doing so, we are able to point to drawbacks in structural studies on river phytoplankton.

Materials and methods

This analysis is based upon literature records of 67 river sites (Table 1). The content lack was reviewed against a checklist of five aspects of community organization, namely, species composition, species richness, dominant species, diversity and biomass (as total biomass and the share of different taxonomical groups). As Table 1 reveals, most studies lack data on the five aspects and this is especially true for tropical rivers. Overall, only studies covering an entire year have been listed – others, of course, do not consider the whole seasonal variability. When several sampling stations have been reported in a single study, we have chosen, where possible, preferring it to be upstream of a tributary confluence. When more than one study has been published for a given site, we have chosen the most recent one in order to reflect as present condition as possible. The current nomenclature of algal species has been ascertained from standard texts. Only studies reporting algal species by name have been taken into account. Varietal names have been merged into species names. Species richness has been considered to be the total number of species reported from a given site for an annual period.

The planktonic nature of the floras has been ascertained using the information given in standard floristic surveys. We have separated the reported algae according to whether they are eu- or meroplanktic species and tycho- and benthic species (see Hutchinson, 1967: 236–237).

We have also separated data on species richness according to the criterion of river latitude. Thus, we were able to test whether species-richness varies with latitude.

Dominant species have been considered to be those attaining more than 10^7 cells l^{-1} at some time in the annual cycle.

Biomass data are mostly comprised of biovolume estimations and are here computed as an annual for each river (units: mm^3 FW l^{-1}). In order to include two well-known rivers (such as the Orinoco and the Danube in Hungary) we have also calculated biomass from chlorophyll *a* data, assuming a Carbon-to-Chlorophyll ratio of 50 (Harris, 1986) and a Carbon-to-freshweight biomass ratio of 0.1 (Nalewajko, 1966). The latter figure should be considered cautiously, especially concerning diatoms (Reynolds, 1984: p. 32). Overall, we have been able to compute biomass averages for 19 rivers.

Diversity indices are not given in most studies. Nevertheless, where tables showing counts of phytoplankton units were included in the original paper, we could calculate them in some instances. The diversity values used here are based upon individuals (either cells, colonies, trichomes and so on) and the units are bits ind^{-1}. Biomass-based diversity values are reported seldomly (but see Descy, 1993) and hence are not considered here.

Finally, the relative biomass of diatoms *vs* time has been used (when available) to ascertain the time course of the main taxonomic group in temperate and tropical rivers. Data have been averaged for each month and for each relevant dataset.

Results

Concerning species occurrence through the entire listing of 50 rivers (Table 1), it is perhaps surprising that many taxa (>50%) have been recorded only once. The average species richness amounts to 126. The wide scatter of river-specific richness is skewed to the left (Fig. 1). The most frequent species (*i.e.*, those reported in more than 50% out of total studies) are: *Asterionella formosa* Hassall, *Aulacoseira granulata* (Ehrenb.) Simonsen, *Cyclotella meneghiniana* Kütz., *Fragilaria capucina* Desmaz., *F. ulna* (Nitzsch) Lange-Bertalot, *Melosira varians* C. Agardh, *Nitzschia acicularis* (Kütz.) W. Smith, *Actinastrum hantzschii* Lagerheim, *Ankistrodesmus falcatus* Corda (Ralfs), *Pediastrum duplex* Meyen, *Scenedesmus acuminatus* (Lagerheim) Chodat and *S. quadricauda* (Turpin) Bréb. No statistically significant relationship between species richness and latitude was found.

When considering the main taxonomic groups, diatoms and green algae account for most species richness in the full data set, being followed by desmids and blue-green algae (Fig. 2, Table 2). However, if we segregate the floras according to whether they are primarily euplanktonic/meroplanktonic, tychoplanktonic or benthic, we can see that the numbers of planktonic species and benthic species are similar. Furthermore, green algae make up half the species richness of the former whereas diatoms overwhelmingly dominate the benthic and tychoplanktonic fraction (Fig. 2). However, the number of euplanktonic diatoms must be surely underestimated because several important species have been likely reported under the epithet of *Stephanodiscus hantzschii*.

The average number of species in temperate rivers appears to be much higher than that of tropical rivers (Fig. 3) but its variability is also higher. However, the small number of tropical rivers studied up to date suggests that this comparison should be considered cautiously. In temperate rivers the share by algal groups is more or less the same shown in the overall compar-

Table 1. Studies used in this overview. The structural features reported of phytoplankton communities are shown; Y: data on the feature; N: no data. Species composition is considered not to be reported if not all species names are reported. Diversity values, when considered to exist, are not always as such in the studies reported but can be calculated easily from raw data. Biomass data can be reported both as total biomass (T) and taxonomic groups biomass (G).

River	Reference	Species Composition	Species Numbers	Species Dominance	Diversity	Biomass T/G
Andriandrano-Mandraka (Madagascar)	Ramanankasina (1978)	Y	Y	N	N	N
Angara (Russia)	Kozova *et al.* (1982)	Y	Y	Y	N	N
Bagoé (Ivory Coast)	Iltis (1982a, b)	N	N	N	Y	Y/Y
Bandama (Ivory Coast)	Iltis (1982a, b)	N	N	N	Y	Y/Y
Blue Nile (Sudan)	Talling & Rzóska (1967)	N	N	Y	N	N
Bure (U.K.)	Moss *et al.* (1984)	Y	N	N	N	Y/N
Caroní (Venezuela)	Sánchez & Vasquez (1989)	Y	Y	N	N	N
Comoé (Ivory Coast)	Iltis (1982a, b)	N	N	N	Y	Y/Y
Connecticut (USA)	Colt (1974)	Y	Y	N	N	N
Cruces (Chile)	Dürrschmidt (1980)	N	Y	Y	Y	N
Danube						
(Austria)	Czernin-Chudenitz (1966)	N	N	Y	Y	N
(Germany)	Steinberg *et al.* (1987)	N	N	Y	N	N
(Slovakia)	Hindák & Durkoviková (1977)	Y	Y	N	N	N
(Hungary)	Kiss (1987)	Y	Y	Y	Y	N
(Rumania)	Enaceanu (1964)	Y	Y	N	N	N
Daugava (Letonia)	Kumsare (1967)	Y	Y	Y	N	N
Dnieper (Ukrainia)	Priimachenko (1981)	Y	Y	Y	N	N
Ebro (Spain)	Sabater & Muñoz (1990)	Y	Y	Y	Y	N

Table 1 (cont.)

River	Reference	Species Composition	Species Numbers	Species Dominance	Diversity	Biomass T/G
Elizabeth (USA)	Marshall (1968)	Y	Y	Y	Y	N
Ely (U.K.)	Esho & Benson-Evans (1984)	Y	Y	N	N	N
Enisei (Russia)	Priimachenko & Bazenova (1990)	N	Y	N	N	N
Ganges (India)	Lakshminarayama (1965)	N	Y	Y	N	N
Geeste (Germany)	Behre (1961) Hustedt (1959)	Y	Y	N	N	N
Guadalquivir (Spain)	López Peral (1987)	Y	Y	Y	Y	N
Hunte (Germany)	Behre (1961) Hustedt (1959)	Y	Y	N	N	N
Irtish (Russia)	Levadnaja *et al.* (1986)	N	Y	N	N	N
Kem (Russia)	Trifonova (1973)	Y	Y	N	N	N
Kolima (Russia)	Kuzmin (1985)	Y	Y	N	N	N
Lafayette (USA)	Marshall (1968)	Y	Y	Y	Y	N
Léraba (Ivory Coast)	Iltis (1982a, b)	N	N	N	Y	Y/Y
Little Miami (USA)	Weber & Moore (1967)	N	N	N	N	Y/Y
Lot	Dauta (1975)	Y	Y	Y	N	Y/N
(France)	Capblancq & Dauta (1978)	Y	Y	N	N	Y/Y
Main (Germany)	Lange-Bertalot (1974)	Y	Y	Y	N	N
Maraoué (Ivory Coast)	Iltis (1982a, b)	N	N	N	Y	Y/Y
Meuse (Belgium)	Descy & Gosselain (pers. comm.)	Y	Y	Y	Y	Y/Y
Mississippi (USA)	Huff (1986)	N	Y	Y	N	Y/Y
Moosi (India)	Venkateswarlu (1969)	Y	Y	Y	N	N
Moselle (France)	Descy (1993)	N	N	N	Y	N
	Descy & Gosselain (pers. comm.)	Y	Y	Y	N	Y/Y

Table 1 (cont.)

River	Reference	Species Composition	Species Numbers	Species Dominance	Diversity	Biomass T/G
Namhan (Korea)	Chung *et al.* (1968)	Y	Y	N	N	N
Neckar (Germany)	Backhaus & Kemball (1978)	Y	Y	Y	N	Y/Y
Negro (Brazil)	Uherkovich (1976)	Y	Y	N	N	N
Neva (Russia)	Raskina (1968)	Y	Y	N	N	N
Nile (Egypt)	Abdin (1948)	Y	Y	N	N	N
Nzi (Ivory Coast)	Iltis (1982a, b)	N	N	N	Y	Y/Y
Obi (Russia)	Levadnaja *et al.* (1986)	N	Y	N	N	N
Ohio (USA)	Hartman (1965)	N	Y	N	N	N
Oka (Russia)	Ochapkin (1981)	N	Y	N	N	N
Orinoco (Venezuela)	Lewis (1988)	N	N	N	N	Y/N
Oshun (Nigeria)	Egborge (1973)	Y	Y	N	N	N
	Egborge (1974)	N	N	Y	N	N
Pechora (Russia)	Gecen (1973)	Y	Y	Y	N	N
Pukhan (Korea)	Chung *et al.* (1968)	Y	Y	N	N	N
Rhein (Germany)	Backhaus & Kemball (1978)	Y	Y	Y	N	Y/N
Shatt al-Arab (Irak)	Huq *et al.* (1978)	N	Y	N	N	N
Sola (Poland)	Krzeczkowska-Woloszyn & Bucka (1969)	Y	Y	N	N	N
Soyang (Korea)	Chung *et al.* (1968)	Y	Y	N	N	N
Spree (Germany)	Köhler *et al.* (in press)	N	N	Y	N	Y/Y
Susquehanna (USA)	Wagner & Schumacher (1970)	Y	Y	N	N	N
Swale (U.K.)	Holmes & Whitton (1981)	Y	Y	Y	N	N
Tapajós (Brazil)	Uherkovich (1976)	Y	Y	N	N	N

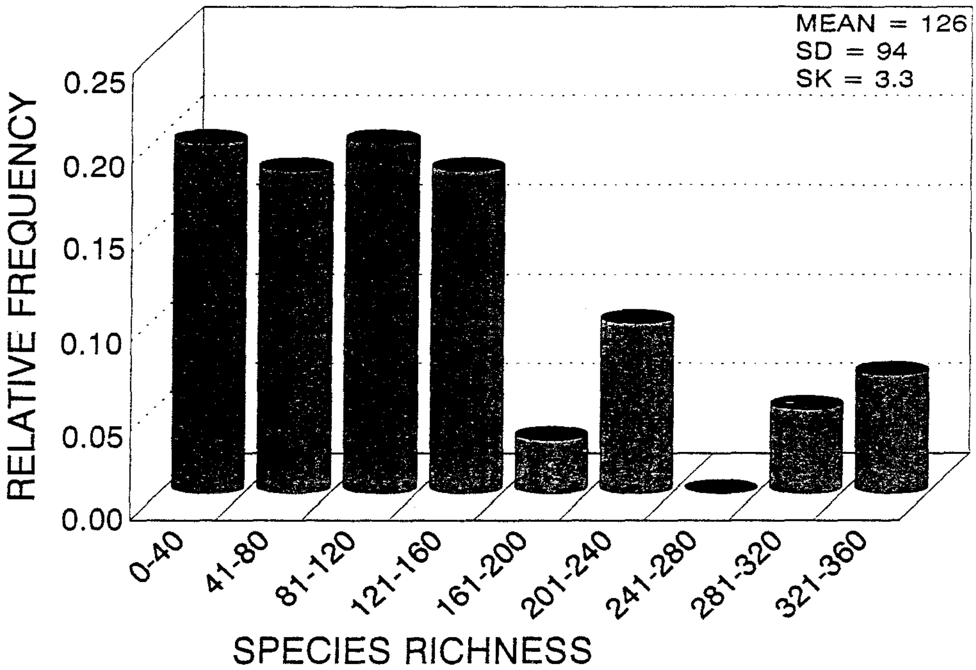
MEAN = 126
SD = 94
SK = 3.3
RELATIVE FREQUENCY
0.25
0.20
0.15
0.10
0.05
0.00
0-40
41-80
81-120
121-160
161-200
201-240
241-280
281-320
321-360
SPECIES RICHNESS

Fig. 1.

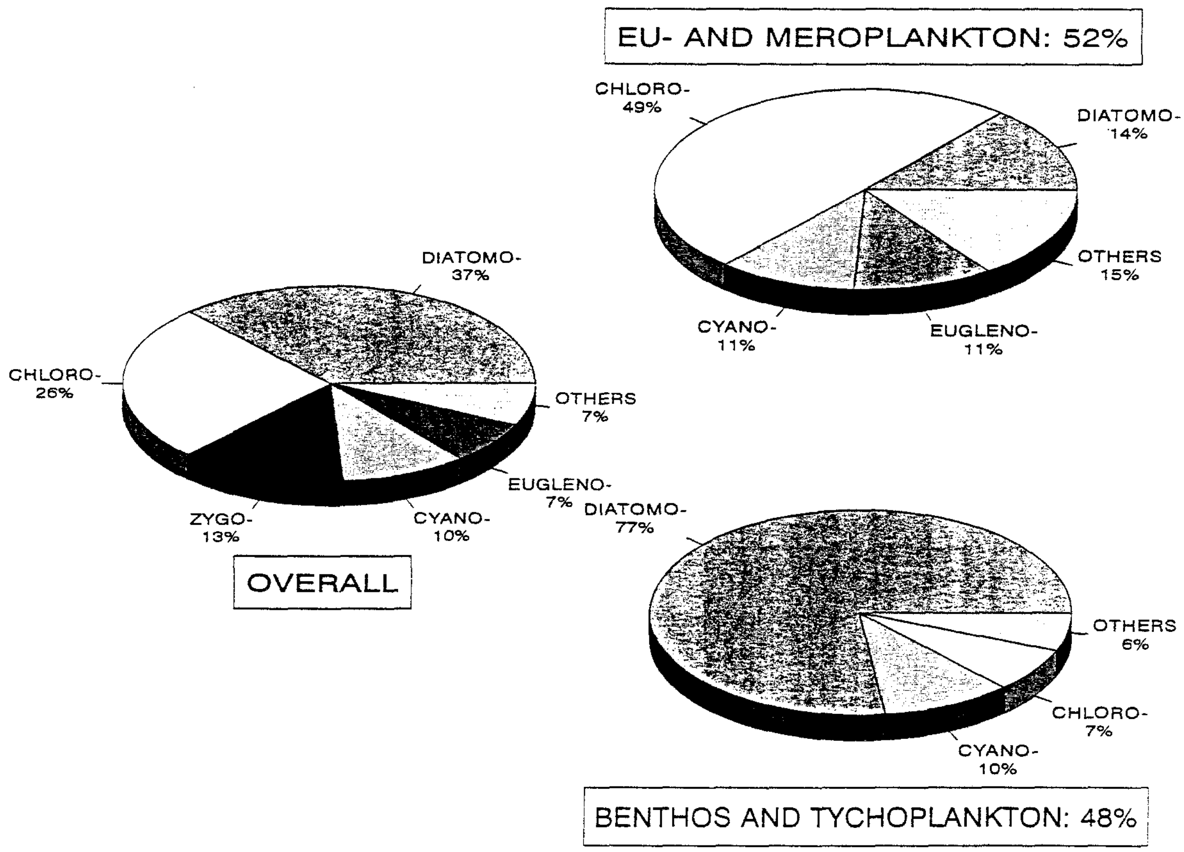
EU- AND MEROPLANKTON: 52%
CHLORO-
49%
DIATOMO-
14%
OTHERS
15%
CYANO-
11%
EUGLENO-
11%
DIATOMO-
37%
CHLORO-
26%
OTHERS
7%
EUGLENO-
7%
ZYGO-
13%
CYANO-
10%
OVERALL
DIATOMO-
77%
OTHERS
6%
CHLORO-
7%
CYANO-
10%
BENTHOS AND TYCHOPLANKTON: 48%

Fig. 2.

Table 1 (cont.)

River	Reference	Species Composition	Species Numbers	Species Dominance	Diversity	Biomass T/G
Tees (U.K.)	Holmes & Whitton (1981)	Y	Y	Y	N	N
Thames (U.K.)	Rice (1938)	Y	Y	N	N	N
	Lack (1971)	N	N	Y	N	Y/Y
Tigris (Irak)	Antoine (1983)	Y	Y	N	N	N
Tisza (Hungary)	Kiss (1974)	Y	Y	Y	Y	N
Tiszalök (Hungary)	Kiss (1974)	Y	Y	Y	Y	N
Tyne (U.K.)	Holmes & Whitton (1981)	Y	Y	Y	N	N
Ural (Russia)	Porjadina (1973)	Y	Y	Y	N	N
Vistula (Poland)	Pajak & Kiss (1990)	Y	Y	Y	N	N
Volta (Ghana)	Biswas (1968)	Y	Y	N	N	N
Wear (U.K.)	Holmes & Whitton (1981)	Y	Y	Y	N	N
Weser (Germany)	Behre (1961) Hustedt (1959)	Y	Y	N	N	N
White Nile (Sudan)	Prowse & Talling (1958)	N	N	Y	N	Y/N
Wye (U.K.)	Jones (1984)	Y	Y	Y	N	N
Yamuna (India)	Rai (1974)	Y	Y	N	N	N

Table 2. Species richness in the whole data set.

	Nr. species
Chlorophyceae	385
Chrysophyceae	43
Cryptophyceae	25
Cyanophyceae (Cyanobacteria)	141
Diatomophyceae	408
Dinophyceae	27
Euglenophyceae	112
Xanthophyceae	11
Zygophyceae (Desmids)	221

ison (Fig. 2), whereas in tropical rivers the number of desmid species is slightly higher than that of diatoms or green algae.

Most blooming species in river phytoplankton are diatoms, with dominant *Stephanodiscus hantzschii* and *Cyclotella meneghiniana* population being reported most frequently (Table 3). However, *S. hantzschii* must have been reported as a group and not as species (Padisák, pers. comm.). It is interesting that most blooming species do not appear to be those most often recorded (see above and Table 3).

The annually averaged biomass distribution of river phytoplankton is certainly low and also skewed to the left (Fig. 4). There are not many data on the biomass

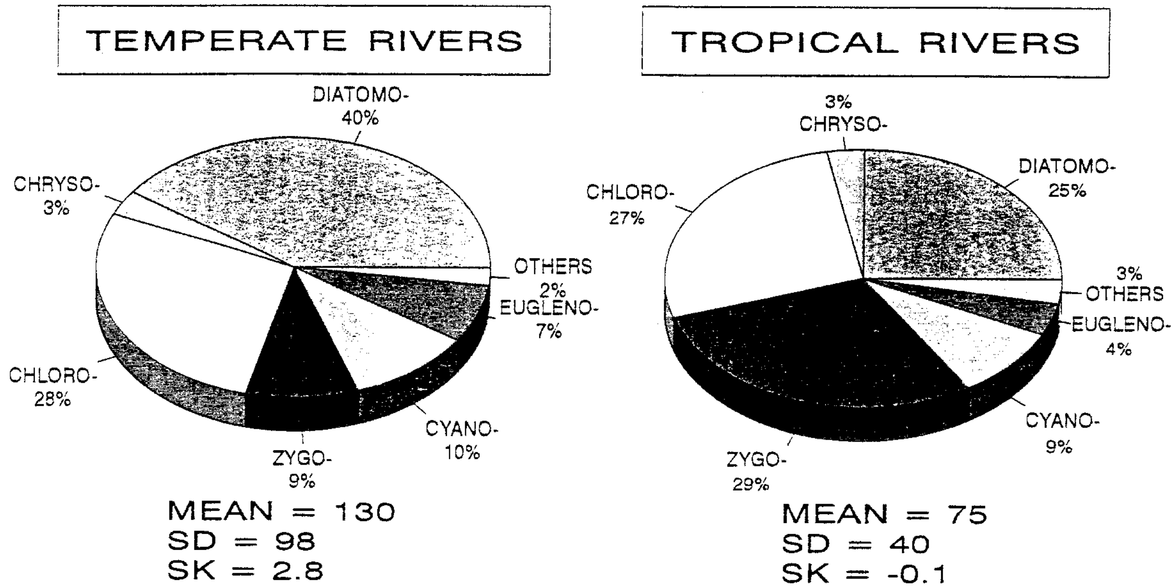

Fig. 3.

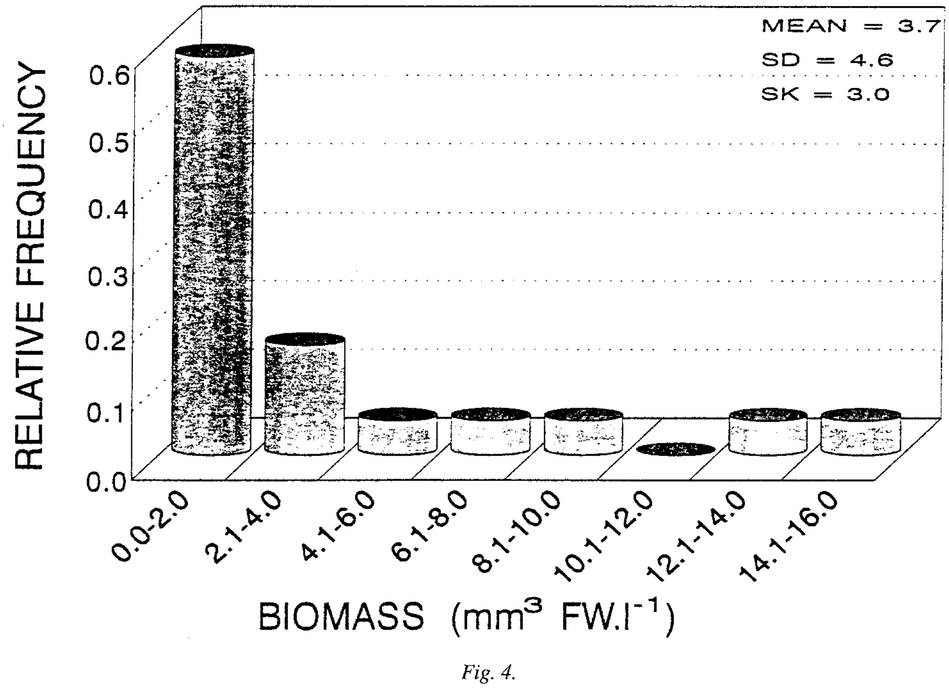

Fig. 4.

partitioning among the main taxonomic groups for river phytoplankton (Table 4). Throughout the year, diatoms appear to be the main group in temperate (69± 15%) and tropical rivers (35± 16%). Taxonomic groups sharing dominance with diatoms are quite different as Table 4 reveals. However, this statement should be considered as provisional for tropical rivers since their data set covers a small geographical area (the rivers of Ivory Coast; Iltis, 1982a). Diatoms in temperate rivers attain dominance after a longer lag than in tropical rivers (Fig. 5).

Diversities of riverine phytoplankton floras range from 0.40 to 4.40 bits ind^{-1}. Overall, they appear to be highly variable (Table 5).

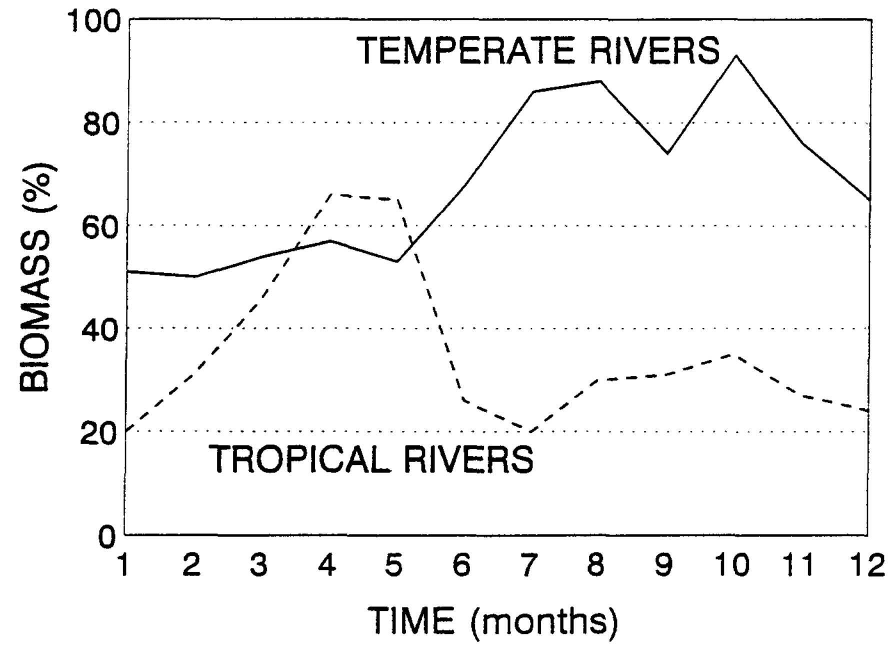

Fig. 5.

Discussion

The structural features of riverine phytoplankton are still poorly known since most reports rely upon reported species composition. The knowledge of temperate rivers and their phytoplankton is much greater than that of tropical rivers and we advocate here increasing efforts in the latter if a broader and more complete knowledge on riverine phytoplankton is desired.

There is also another drawback in potamoplankton structural studies and this is the lack of data on size distributions. To our knowledge no such study has been yet carried out.

However, some features can be found that make phytoplankton community structure in rivers different from that found in standing waters. For example, there is a high incidence of sporadic species in rivers, part of which – of course – can be attributed to taxonomical inadequacies. In common surveys of lake phytoplankton the share of sporadic species is usually not so high. Only when one is carrying out more thorough surveys are a lot of sporadic species recorded (Padisák, 1992). Anyway, most lake sites reported in the latter study are turbid and hence share many ecological features with rivers, as this workshop reveals. Therefore, it might be suggested that river phytoplankton has a big ecological memory, sensu Padisák (1992), not to mention the benthic floras as a 'seed bank' (Liepolt, 1961).

Another conspicuous feature is the dominance of diatoms in species numbers (Fig. 2) as well as in biomass (Fig. 5). The causes for this has been clearly outlined by Reynolds (1994) and we shall not deal with them here. Also, the relative biomass of diatoms is much higher in rivers than in most lakes (Alvarez Cobelas & Rojo, 1994) and since relative biomass is an index of the successful competitive abilities to exploit a given environment (Sommer, 1989) diatoms appear to be the best adapted taxonomic group for living in the highly unstable riverine environment.

Average biomass is another distinguishing feature between lake and river phytoplankton. In lakes its range is broader (0.02–100 mm^3 FW l^{-1}, Smith, 1990) than in rivers (0.06–25 mm^3 FW l^{-1}, Fig. 5) and the existence of many hypertrophic lakes around the world makes averaged biomass lower in rivers. This does not dismiss the fact the rivers can support very high concentrations of phytoplankton at times (Kiss, 1987; López Peral, 1987; Prowse & Talling, 1958; Reynolds *et al.*, 1991). Anyway, data on phytoplankton biomass are still scarce for rivers as compared with those of lakes.

Tropical rivers appear to have different phytoplankton community structure from temperate rivers.

Table 3. Blooming species in river phytoplankton.

River	Taxa	Reference
Danube (Germany)	*Cyclotella pseudostelligera* Hustedt	Steinberg *et al.* (1987)
Danube (Hungary)	*Cyclotella meneghiniana* Kütz. *Stephanodiscus hantzschii* Grun. *Stephanodiscus parvus* Stoermer et Håkansson	Kiss (1987)
Ebro	*Pediastrum duplex* Meyen	Sabater & Muñoz (1990)
Elizabeth	*Cylindrotheca closterium* Reimann et Lewin *Skeletonema costatum* (Grev.) Cleve	Marshall (1968)
Ganges	*Aulacoseira granulata* (Ehrenb.) Simonsen *Cyclotella meneghiniana* Kütz. *Microcystis aeruginosa* Kütz.	Lakshminarayana (1965)
Guadalquivir	*Chroococcus limneticus* Lemm.	López Peral (1987)
Lafayette	*Skeletonema costatum* (Grev.) Cleve	Marshall (1968)
Main	*Stephanodiscus hantzschii* Grun.	Lange-Bertalot (1974)
Meuse	*Cyclotella pseudostelligera* Hustedt *Stephanodiscus hantzschii* Grun. *S. tenuis* Hustedt	Descy & Gosselain (pers. comm.)
Mississippi	*Aulacoseira italica* (Ehrenb.) Simonsen	Huff (1986)
Moselle	*Cyclotella meneghiniana* Kütz. *Skeletonema potamos* (Weber) Hasle	Descy (1993)
Neckar	*Stephanodiscus hantzschii* Grun.	Backhaus & Kemball (1978)
Thames	*Stephanodiscus hantzschii* Grun.	Lack (1971)
Wear	*Cyclotella meneghiniana* Kütz.	Holmes & Whitton (1981)
Wye	*Cyclotella pseudostelligera* Hustedt	Jones (1984)

Diatoms are not dominant in species numbers (Fig. 3), being substituted by desmids, and their share of relative biomass is much lower (Fig. 5), though still likely dominant. It is unsafe to speculate about the causes for this since we only rely on data from a small geographical, tropical area (Iltis, 1982a, 1982b): it might be longer photoinhibition effects or lower tolerance to higher water temperatures. Anyway, diatom dominance follows different time courses in temperate and tropical rivers and dominance is not only shared with green algae (Table 4) as many studies suggest.

Acknowledgments

A literature review like this has been benefitted from the searching help of some friends, who have sent us a great deal of preprints and works published in serials difficult to be found in Spain. These friends are Irina Trifonova, Keve Kiss, Antal Schmidt, Horst Lange-Bertalot, Amelia Gómez Garreta, Tomás Gallardo, Jan Köhler, Teresa López Peral and Joan Lluis Riera. Furthermore, we have been gifted with very complete, albeit not entirely published yet, data sets on

Table 4. Main taxonomic groups sharing biomass dominance with diatoms in river phytoplankton. See also Fig. 5.

River	Algal group	Reference
Bagoé	Euglenophyceae	Iltis (1982b)
Bandama	Mixed assemblage	Iltis (1982b)
Comoé	Euglenophyceae + Dinophyceae	Iltis (1982b)
Léraba	Euglenophyceae	Iltis (1982b)
Little Miami	Chlorophyceae	Weber & Moore (1967)
Lot	Chlorophyceae	Capblancq & Dauta (1978)
Maraoué	Mixed assemblage	Iltis (1982b)
Meuse	Chlorophyceae	Descy & Gosselain (pers. comm.)
Mississippi	Cyanophyceae	Huff (1986)
Neckar	Chlorophyceae	Backhaus & Kemball (1978)
Nzi	Mixed assemblage	Iltis (1982b)
Spree	Cyanophyceae	Köhler (1993)

Table 5. Diversity of river phytoplankton (bits ind^{-1}).

River	Mean	SD	Range	Reference
Bagoé	2.39	0.86	1.20–3.51	Iltis (1982b)
Comoé	2.02	0.82	1.02–3.54	Iltis (1982b)
Danube (Austria)	2.20	1.09	0.98–3.92	Czernin-Chudenitz (1966)
Danube (Hungary)	2.50	0.17	2.30–2.69	Kiss (1987)
Ebro	1.54	0.77	0.43–2.99	Sabater & Muñoz (1990)
Elizabeth	0.84	0.40	0.38–1.32	Marshall (1968)
Guadalquivir	3.07	0.88	2.25–4.38	López Peral (1987)
Lafayette	1.36	0.63	0.75–2.02	Marshall (1986)
Léraba	1.80	0.48	1.02–3.08	Iltis (1982b)
Meuse	1.86	1.18	0.72–3.95	Descy & Gosselain (pers. comm.)
Moselle	2.96	0.77	1.20–3.80	Descy (1993)
Tisza	0 70	0.44	0.40–1.20	Kiss (1974)
Tiszalök	1.42	0.38	1.04–1.81	Kiss (1974)

the rivers Meuse and Moselle by Jean Pierre Descy and Véronique Gosselain. Also, some copies of difficult-to-be-found studies have been supplied to us by the CSIC libraries (Spain), the Univ. Valencia library and the FBA library (Windermere, UK). The comments, criticisms and suggestions by Colin Reynolds, Judit Padisák, Jean Pierre Descy and two anonymous referees have improved the final draft of the manuscript. We are very grateful to all of them.

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