Phytoplankton growth in three rivers: The role of meroplankton and the benthic retention hypothesis

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Abstract

We analyzed long-term (5–8 yr) hourly time series of chlorophyll (Chl) converted from fluorescence measurements in relation to discharge and light in three medium- to large-size rivers, where planktonic diatoms dominated during the growing season. Overall, there was an inverse relationship between discharge and Chl. At fine temporal scales, flow pulses were typically accompanied by an increase in diatom Chl. In contrast, chlorophytes were usually diluted. The increase in diatoms was likely due to resuspension of meroplanktonic species from the bottom. The benthic retention hypothesis proposes that rapidly sedimenting diatoms take advantage of a prolonged benthic residence provided that the enhanced retention is sufficient to compensate for slower light-supported growth at the bottom relative to water. This hypothesis was tested with simple growth models. Although the rivers were highly turbid and did not support net growth when flow exceeded a rather low threshold, benthic retention might have favored low-light–adapted algae during more than half of the period when net growth was possible. Among the physical factors, the rate of resuspension might be the critical factor that determines the ultimate success of a meroplanktonic life cycle strategy. The three rivers of this study rarely supported persistent planktonic populations. We propose that self-sustaining populations of riverine algae are primarily based on meroplanktonic diatom species, whereas truly planktonic populations, mostly chlorophytes, depend on periodic inoculations from out-of-channel sources.

Explanations for the origin, persistence, and growth of fluvial phytoplankton under conditions of an essentially unidirectional flow have been a major intellectual challenge for fluvial ecologists and led Reynolds (1988) to distill the essence of the problem into the "paradox of potamoplankton." In their review of phytoplankton of large rivers, Reynolds and Descy (1996) hypothesized that reach-scale retention could account for the observed rates of downstream recruitment of growing populations, and noted that this hypothesis did not provide an answer to the question of how non- or slow-growing cells can avoid washout. They proposed a mechanism of overwintering resting stages of meroplanktonic species (having the ability to pass a part of the life cycle settled on the bottom) in relatively fine-grained deposits (e.g., sand and silt). Subsequently, Stoyneva (1994) deduced from long-term phytoplankton records that shallow bottoms were important source areas of phytoplankton inoculation along the lower reaches of such a large river as the Danube. Convincing field evidence validating the role of aggregated dead zones (ADZs) as retentive habitats, however, was scarce, as were studies indicating an important role of meroplankton in rivers (Reynolds 2000).

Meroplankty (Reynolds 2000) is a type of life history adaptation characteristic of several diatom species that inhabit the highly energetic environment of shallow, turbid, polymictic lakes. Such species may dominate during windy summers (Padisák 1992; Honti et al. 2007) or during other times when there is wind-induced resuspension (Padisák and Dokulil 1994; Schelske et al. 1995). Carrick et al. (1993) argued that meroplanktonic diatoms in Lake Apopka, Florida, were planktonic species adapted to survive long periods on an aphotic bottom by forming resting propagules that quickly rejuvenated upon light exposure when resuspended. Although some of these studies emphasized that shallow lakes were as turbid as many large rivers (Padisák and Dokulil 1994), they failed to inspire fluvial phytoplankton ecologists to systematically explore the feasibility of meroplankty in flowing waters. The cause of ignorance might be the commonly observed light deficiency of phytoplankton in most rivers (Vannote et al. 1980; Dokulil 1994; Reynolds and Descy 1996), the channels of which are often much deeper than the mean depth of shallow lakes that accommodate meroplanktonic diatoms. Therefore, the first step towards the validation of a benthic retention mechanism and meroplankty to support self-sustaining phytoplankton populations should include a systematic evaluation of phytoplankton dynamics in relation to the interrelated set of flow and light conditions.

In this study we analyze long-term, hourly records of fluorometric chlorophyll (Chl) in relation to flow and turbidity from three medium- to large-size rivers. Our hypothesis was that meroplanktonic algae might gain an advantage over planktonic algae if prolonged benthic residence relative to washout compensates for diminished light availability on the bottom. We examine this hypothesis with simple growth models, and then compare meroplanktonic and truly planktonic populations in terms of inoculation and persistence in advective environments, to provide a more comprehensive statement of the original hypothesis.

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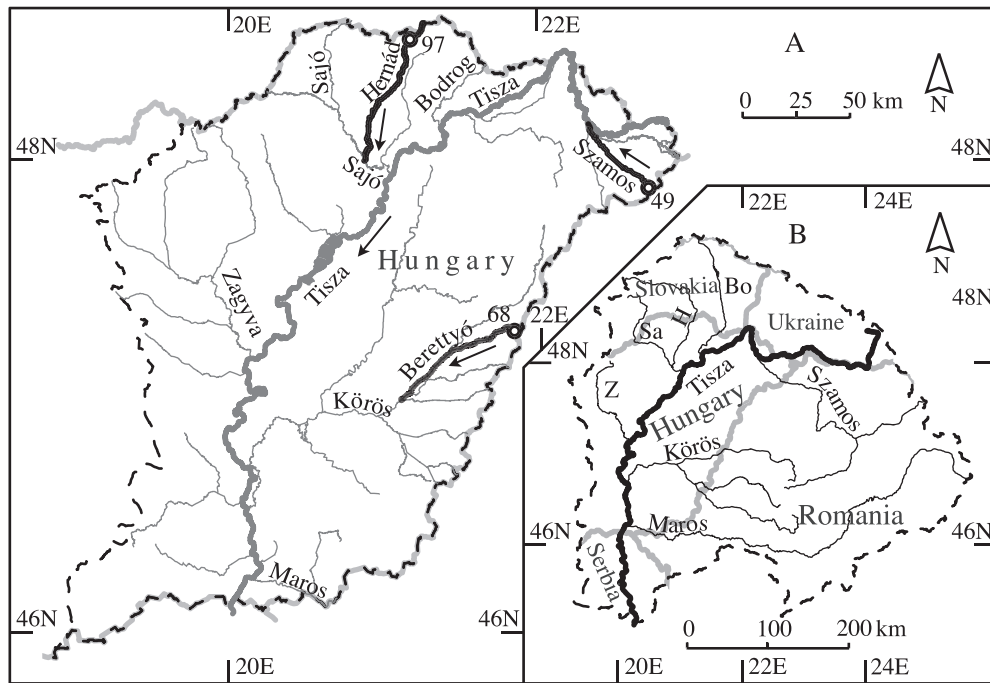
Fig. 1.   (A) Monitoring sites (B) in the catchment of the Tisza River. (A) The Berettyó, Hernád, and Szamos Rivers and (B) the Tisza River are shown with thick lines. Arrows indicate flow direction.

Methods

Study sites—We used time series of the online water quality monitoring and alarm network (www.rivermonitoring.hu) that has operated since 2002 near the border sections of the Berettyó (river km 68), Hernád (river km 97), and Szamos Rivers (river km 49; Fig. 1). The three rivers belong to the Tisza River network, the latter being the largest tributary of the Danube (Fig. 1). Entering Hungary, the rivers are highly polluted with both industrial effluent and municipal sewage (Sárkány-Kiss and Hamar 1999; Sárkány-Kiss et al. 1999; Table 1). Besides chronic pollution, fatal accidents threaten the ecological integrity of these systems, including repeated oil seepage into the Berettyó River (Sárkány-Kiss et al. 1999) and cyanide and heavy metal spills in the Szamos River (World Wide Fund for Nature 2002). The Szamos, comparable in size to the upper Tisza River, is the dominant influence on water quality along the Hungarian section of the Tisza River (Istvánovics et al. 2010).

The rivers differ in size, trophic status (Table 1), and degree of regulation. In Romania, the Someş River (the Hungarian Szamos) is a more or less unregulated river with alternating constrained and braided reaches. In contrast, the Berettyó River (the Romanian Barcău) has been channelized along its 40–50 km of lowland section upstream of the monitoring site. The Ér River (the Romanian Ier) enters the Berettyó close to the monitoring site and represents about 20% of total discharge. The Ér River has several mainstream reservoirs. The flow of the Hernád River (the Slovakian Hornád) is strongly influenced by a series of upstream reservoirs and bottom sills.

These constructions heavily modify, but do not eliminate, the riffle and pool sequences in the river.

In the Szamos River, planktonic diatoms (*Thalassiosira* and *Stephanodiscus* spp.) dominate from May to late October. They are replaced by benthic diatoms during the spring and presumably in the winter (Istvánovics et al. 2010; L. Vörös unpubl.). In the Hernád River, *Stephanodiscus hantzschii* is overwhelmingly dominant during the summer (North-Hungarian Inspectorate for Environment, Nature Conservation and Water unpubl. data). In the Berettyó River, planktonic diatoms (*Cyclotella meneghiniana, Stephanodiscus minutulus, Nitzschia acicularis*) and/or Chlorococcales dominate. The biomass of benthic diatoms rarely exceeds that of planktonic diatoms, even during the cold season (G. Borics unpubl. data).

Data collection and handling—Water was pumped into riverbank monitoring stations every hour from 30 cm below the water surface from the thalweg. The pumped volume was sufficiently large to thoroughly rinse the sampling system before taking a representative fresh river sample. Temperature and turbidity were measured with a multiparameter probe (Sensortechnik Meinsberg GmbH). The pigment fingerprint of phytoplankton was recorded from direct fluorescence (bbe Moldaenke GmbH). Total Chl was partitioned among four groups of phytoplankton ("diatoms," i.e., chromophytes including both diatoms and dinoflagellates; chlorophytes; cyanobacteria; cryptophytes) using custom software provided by the manufacturer.

Hourly time series of Chl, turbidity, and water temperature were downloaded from the open access database of the monitoring network. These records were screened for

Table 1. Physical variables, nutrient concentrations, and Chl at the online monitoring sites. Discharge was calculated from daily averages in the period 2002 and 2009. Water quality data represent weekly to biweekly records of the National Water Quality Database. TP, total phosphorus measured as SRP after H_2SO_4–H_2O_2 digestion; SRP, soluble reactive phosphorus, molybdenum blue method; DIN, dissolved inorganic nitrogen; Chl, chlorophyll extracted in hot ethanol, uncorrected for pheophytin.

Variable	Berettyó			Hernád			Szamos		
	Value	Median	Range	Value	Median	Range	Value	Median	Range
Upstream drainage area (km²)	3502			4515			15,283		
Upstream length (km)	127			191			489		
Slope at median Q (m km⁻¹)	0.19			0.90			0.22		
Bottom deposit	Clay, silt			Fine gravel			Coarse sand		
Discharge (Q, m³ s⁻¹)		4.9	1.4–134		21.8	6.1–525		90	15.7–1157
Suspended solids (g m⁻³)		31	2–975		26	7–912		50	24–1120
TP (mg P m⁻³)		319	91–2250		310	120–1230		100	40–680
SRP (mg P m⁻³)		60	3–342		222	16–616		59	13–313
Dissolved inorganic N (mg N m⁻³)		1450	140–6230		3550	1490–6440		1200	70–3740
DIN:SRP		21.6	1.4–490		16.0	6.7–65.2		19.8	0.6–580
Chl (mg Chl a m⁻³)		2.9	0.1–166		4.0	0.1–69		4.8	0.1–369

consistency, and online measurements were also compared with standard weekly to biweekly monitoring data stored in the National Water Quality Database. Statistical properties of the screened time series are summarized in Table 2. To decrease measurement noise, we used a 3-h moving average of turbidity. To remove variability caused by the diurnal cycle in the photosynthetic status of algae, we calculated a 24-h moving average of fluorometric Chl.

Hourly records of stage height were obtained from regional water authorities. A small number of missing data were obtained by linear interpolation from nearest neighbors. Discharge (Q, m³ s⁻¹) was estimated from the rating curves of gauging stations. The gauging station positions coincided with the online water quality monitoring sites in the case of the Berettyó and Szamos Rivers, whereas the nearest gauge was 1.5 km upstream in the Hernád River.

Simple models of phytoplankton growth—Our benthic retention hypothesis requires that the residence time of settled cells (τ_b, s) exceeds that of advecting cells (τ_W, s) to compensate for slower growth stemming from reduced light exposure at the bottom. Simple growth models were developed to examine whether this condition was fulfilled in the rivers of study.

We begin by considering a truly planktonic alga growing only in the water at a rate G_p (s⁻¹). Neglecting losses other than basal respiration (R_p, s⁻¹), the change in local biomass (B_p, mg Chl m⁻³) in a homogeneously mixed section of length L (m) can be written as

$$\frac{dB_p}{dt} = -\frac{1}{\tau_w} \times \left(B_p - B_{p,in}\right) + B_p \times \left(G_p - R_p\right) \quad (1)$$

where t (s) is time and $B_{p,in}$ (mg Chl m⁻³) is the inflow biomass at the upstream boundary. If cells are advected at the mean velocity of water (v, m s⁻¹), the retention time is given by $\tau_w = L/v$.

For a meroplanktonic species, changes in the planktonic (B_p, mg Chl m⁻³) and benthic biomass (B_b, mg Chl m⁻²)

are tightly coupled. Assuming that (1) the rate of settling (v_s, m s⁻¹) is constant, (2) resuspension is a function of shear stress that, in turn, is proportional to v^2, and (3) resuspension also depends on the benthic population size, the following equations apply:

$$\frac{dB_p}{dt} = -\frac{1}{\tau_w} \times \left(B_p - B_{p,in}\right) + B_p \times \left(G_p - R_p\right)$$

$$\times -\frac{v_s}{Z} \times B_p + \frac{k_{resusp} \times v^2}{Z} \times B_b \quad (2a)$$

$$\frac{dB_b}{dt} = v_s \times B_p - k_{resusp} \times v^2 \times B_b + B_b \times \left(G_b - R_b\right) \quad (2b)$$

where k_{resusp} (s m⁻²) is a proportionality factor and Z (m) is mean cross-sectional depth. From Eq. 2b, $\tau_b = 1/(k_{resusp} \times v^2)$.

Equation 2 allows for formalizing the prerequisite conditions for successful meroplanktonic adaptation. Defining a day as the period between successive sunrises, hourly net growth rates averaged over a day must be positive at the bottom when the daily average is positive in the water:

$$\text{if} \quad \overline{\left(G_p - R_p\right)} > 0 \text{ and } \overline{\left(G_b - R_b\right)} > 0 \quad (3a)$$

$$\text{then} \quad \overline{\tau_b} \times \overline{\left(G_b - R_b\right)} \geq \overline{\tau_w} \times \overline{\left(G_p - R_p\right)} \quad (3b)$$

where overline denotes a daily average.

Nutrients are not likely to limit growth in the nutrient-rich rivers of study (Table 1; though silica concentrations are unknown), therefore we consider only temperature (T, °C) and light (I, μmol quanta m⁻² s⁻¹) limitation:

$$G = G_{max} \times f(I) \times f(T) \quad (4)$$

where G_{max} is the maximum growth rate at optimal light and temperature, $0 < f(T) \leq 1$, and $0 < f(I) \leq 1$ are

Table 2. Statistical properties of the screened hourly time series. T, water temperature.

Variable	Berettyó	Hernád	Szamos
Starting date of valid records	01 Jul 2005	01 Jan 2003	01 Jan 2002
End date	31 Dec 2009	31 Dec 2009	31 Dec 2009*
Missing and unreliable records (% of total)	15	10	25
Water temperature, mean (°C)	12.5	10.8	12.5
Water temperature, SD (°C)	7.8	7.0	8.1
Turbidity, median (NTU)	47.6	45.8	72.2
Turbidity, range (NTU)	1.8–1224	8.5–2206	6.4–1611
Total Chl, median (mg m^{-3})	2.7	0.9	6.7
Total Chl, range (mg m^{-3})	0.1–68.6	0.1–42.5	0.1–329.5
Diatom Chl, median (% of total)	45.7	83.9	65.8
Diatom Chl, range (% of total)	0.0–100	0.0–100	0.0–100
Chlorophyte Chl, median (% of total)	19.4	0.0	6.4
Chlorophyte Chl, range (% of total)	0.0–80.6	0.0–98.1	0.0–100

* No turbidity records were available from July 2004 to July 2005.

dimensionless factors. Basal respiration may have the same temperature dependence as growth, and thus it can be approximated as $R = r \times G_{max} \times f(T)$, where r (dimensionless) is the respired fraction of fixed carbon (Reynolds 1997). Assuming that physiological properties of meroplanktonic cells do not change while residing in the benthos, this simplifies the term $\overline{(G-R)}$ in Eq. 3 to $\overline{(f(I)-r)}$.

Following Bormans and Webster (1999), we chose a Michaelis-Menten type function to express light dependency of growth:

$$f(I) = \frac{I}{I + K_I} \qquad (5)$$

where K_I (μmol quanta m^{-2} s^{-1}) is the half-saturation constant. Although there is no reason to expect a systematic shift in K_I during a sedimentation–resuspension spiral, settled and fully entrained cells are differentially exposed to light (I_Z and I^*, respectively). At the bottom, light exposure will be

$$I_Z = I_0 \times e^{(-K_d \times Z)} \qquad (6)$$

where I_0 is the incident photosynthetically active radiation (PAR) at the water surface and K_d (m^{-1}) is the coefficient of diffuse light attenuation. In a mixed column, average light conditions (I^*) can be approximated as PAR at the middle of the water column (Reynolds 1997):

$$I^* = \sqrt{I_0 \times I_z} \qquad (7)$$

From the last two equations, a bottom light index ($K_d.Z/2$) can be developed to characterize bottom light exposure relative to light exposure in the water:

$$\frac{K_d \times Z}{2} = -\ln\left(\frac{I_z}{I^*}\right) \qquad (8)$$

Application of the growth models—We examined a river section of length $L = 1000$ m. Mean water velocity and depth were estimated from Q using functions derived from

hydraulic properties of the gauged cross sections. Based on data from the Szamos and Tisza Rivers (V. Istvánovics unpubl.), turbidity (nephelometric turbidity units [NTU]) was converted to a coefficient of light attenuation using the relationship $K_d = 0.22 \times NTU^{0.73}$. A similar relationship has been reported from the turbid Adige River, Italy (Salmaso and Zignin 2009).

Hourly I_0 values were calculated using angular functions of solar geometry at our latitude (47.5°N). Maximal I_0 at noon of the summer solstice was set to 1000 μmol quanta m^{-2} s^{-1}. Hourly $f(I_Z) - r$ and $f(I^*) - r$ values were averaged over each day when a complete series of hourly K_d values was available during the light period. The number of such days totaled 1532, 2360, and 2033 in the Berettyó, Hernád, and Szamos Rivers, respectively. Most calculations were performed with a K_I value of 20 μmol quanta m^{-2} s^{-1} and $r = 0.1$. In a sensitivity analysis we tested the effect of K_I (from 10 to 60 μmol quanta m^{-2} s^{-1}) at $r = 0.1$, as well as that of r (from 0.05 to 0.1) at $K_I = 20$ μmol quanta m^{-2} s^{-1}. We checked the effect of separately analyzing data from the half-year periods when planktonic and benthic algae were likely to dominate (May to October and November to April, respectively). The shift in patterns was small; therefore, we present only the results of the year-round analysis.

To test the feasibility of meroplankty in the study rivers, we estimated how many times τ_b should exceed τ_w to balance lower benthic light exposure. To avoid parameterization of such a poorly known process as resuspension of settled algae in rivers, Eq. 3 was both simplified and rearranged into a directly applicable form:

$$\text{if } \overline{(f(I^*)-r)} > 0 \text{ and } \overline{(f(I_Z)-r)} > 0 \qquad (9a)$$

$$\text{then } \left[\frac{\overline{\tau_w}}{\overline{\tau_b}}\right]_{max} = \frac{\overline{f(I_Z)-r}}{\overline{f(I^*)-r}} \qquad (9b)$$

To highlight the significance of meroplankty, we examined the potential persistence of a planktonic population for each river. For this purpose, the persistence criterion of Speirs and Gurney (2001) was used for a

vertically and horizontally mixed river:

$$\tau_w > \frac{\varepsilon}{0.434 \times (G_p - R_P)} \qquad (10)$$

where $0 < \varepsilon \leq 1$ is the fraction of time the organism spends in the bulk flow. Water residence time was calculated from the upstream length (Table 1) and daily mean flow velocity estimated at the monitoring site. Light-limited net growth rate was estimated either considering or neglecting temperature limitation (cf. Eq. 4). The former option introduced additional uncertainty, whereas the latter overestimated the frequency of persistence. For $f(T)$, the sigmoidal function and parameters for diatoms were adopted from Garnier et al. (1995). The maximum growth rate was set to 1.5 d^{-1}. We estimated the frequency of days when a planktonic alga with $K_I = 20$ μmol quanta m^{-2} s^{-1} and $r = 0.1$ could persist in the study rivers.

Results

The study period included years approaching both ends of hydrological extremes (Fig. 2). Seasonal variability of discharge was similar at each site. Spring floods were fed primarily by snowmelt. Heavy summer rains, which were most likely to occur around June, generated numerous additional flow pulses (Fig. 2).

Total Chl varied over 3–4 orders of magnitude in each river (Tables 1, 2). The median value was the highest in the Szamos River—the largest but the least nutrient rich of the three rivers. Diatoms and chlorophytes made up more than two-thirds of total biomass. The latter group was considerably more successful in the Berettyó River than in the other two rivers. Although the largest turbidity peak was observed in the Hernád River, Szamos was the most turbid of our rivers.

Observations pointing towards a benthic retention mechanism—Daily mean Chl was inversely related to daily mean flow when, for comparative purposes, both values were normalized (Chl/Chl$_{max}$, Q/Q_{max}) and averaged over categories with equal numbers of data (Fig. 3). In addition Chl/Chl$_{max}$ was inversely related to normalized turbidity.

In contrast to this pattern based on pooled data, Chl tended to increase more or less simultaneously with Q at hourly time scales. To characterize the fine-scale relation between the two variables, we systematically inspected each flow pulse. A flow pulse was defined rather subjectively as a twofold increase in Q over a reasonably short period of time followed by a relatively monotonous reversal to a quasi-permanent stage. Altogether, 200 flow pulses were identified in the three rivers. In about 80% of cases, total Chl increased with flow. There was substantial variability in the amplitude and timing of turbidity and group-specific Chl relative to flow. Without information about the upstream hydraulic and geometric features, each pulse appeared to be highly specific. Therefore, we identified qualitatively a few recurrent patterns (Fig. 4). None of the patterns was restricted to or occurred more frequently in a particular river, and each example represented the summer
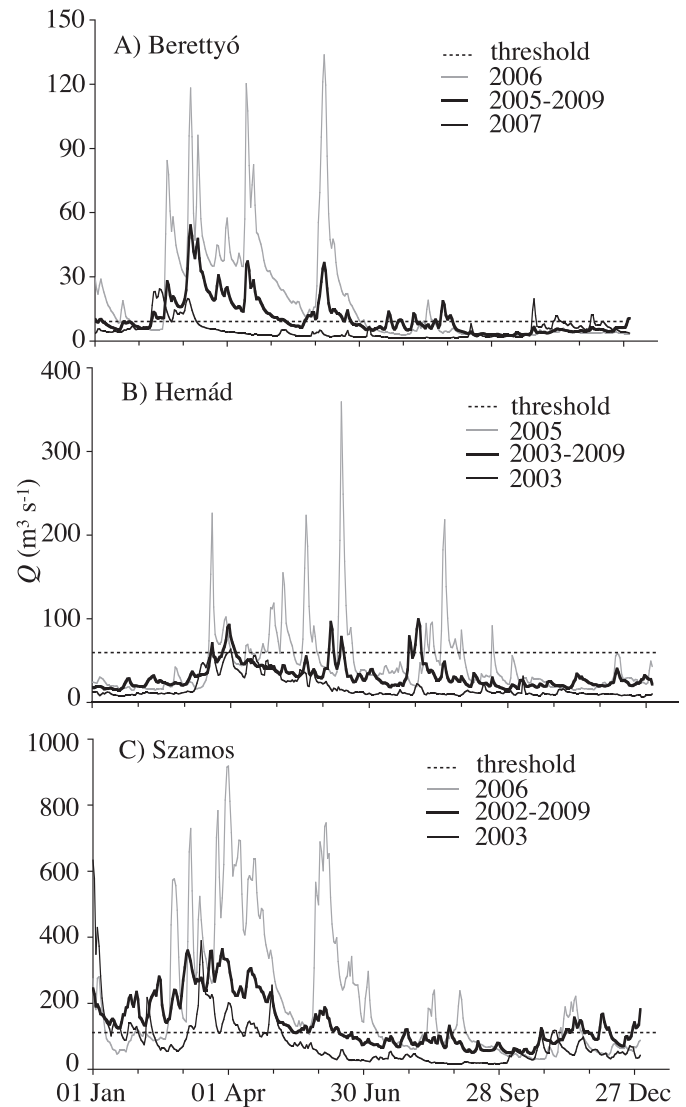

Fig. 2. Seasonal flow pattern in (A) Berettyó, (B) Hernád, and (C) Szamos Rivers. (The driest and wettest years as well as the average for the study period are shown. The annual flow was 159 (driest), 340 (average), and 602 (wettest) million m³ in the Berettyó River; 550, 996, and 1424 million m³ in the Hernád River; and 2515, 4427, and 6300 million m³ in the Szamos River, respectively. Threshold is the approximate flow above which a low-light–adapted planktonic alga is unable to maintain positive net growth; *see* text.)

period, when biomass of benthic and epiphytic species was negligible.

Large flood pulses led to a decrease in the biomass of both diatoms and chlorophytes (Fig. 4A). The biomass of cyanobacteria, however, consistently increased, even during these floods. As seen from the turbidity record, the increase coincided with enhanced sediment resuspension (Fig. 4B). The peak biomass of cyanobacteria remained diminutive, but the increment was conspicuous because this group was nearly always absent from the water at times outside of flow pulses. There was a characteristic hysteresis during each flow pulse (i.e., lower cyanobacteria–Chl : NTU ratio during the rise than during the fall of turbidity). For small
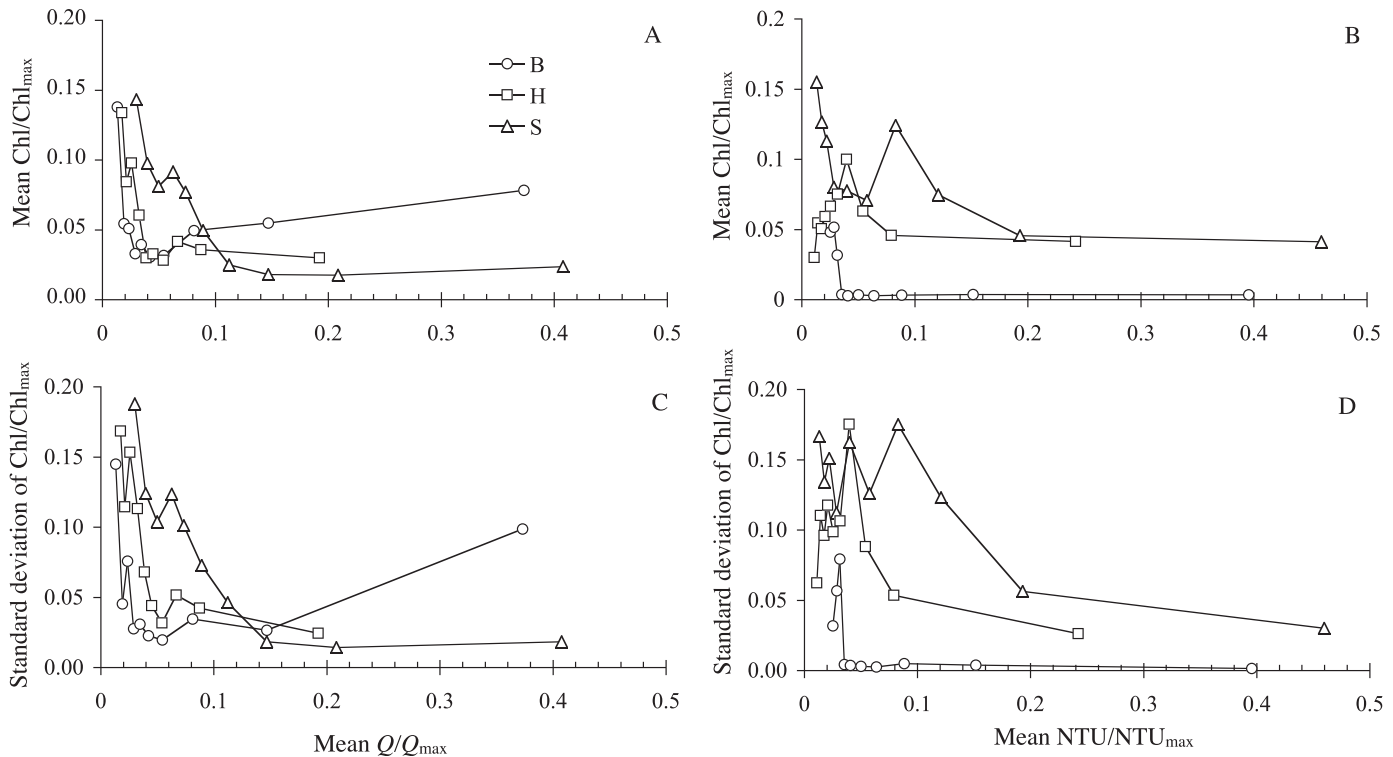
Fig. 3.   (A, B) Mean and (C, D) standard deviation of normalized total Chl as a function of (A, C) normalized mean flow and (B, D) normalized mean turbidity. Normalized values were averaged over categories that contained equal number of data. B, H, S: Berettyó, Hernád, and Szamos Rivers, respectively.

to medium flow pulses the biomass of diatoms increased with increasing Q, whereas chlorophytes usually decreased (Fig. 4C). The last example (Fig. 4D) further illustrates the differences between diatoms and cyanobacteria and suggests that processes that generated these peaks were different.

Considering enhanced dilution, flushing, and sediment resuspension during flow pulses, one might tentatively assume that no growth occurred during these periods. This means that the passing biomass must have been produced and stored somewhere upstream prior to being flushed. A flow-pulse biomass (g Chl) was estimated by summing biomass fluxes ($Q \times$ Chl) from hourly records. Storage in periodically isolated backwaters was neglected. Knowing the median Chl concentration prior to the flow pulse and assuming that the flow-pulse biomass was stored in the dead zone volume that occupied as much as one-third of the total upstream volume, it was possible to derive approximation of lateral heterogeneity that should have been associated with storage. With rare exceptions, the estimates were exceptionally high: Chl concentration in the dead zone volume should have exceeded that in the bulk flow at least two times, and typically was up to several hundred times greater (not shown). The figures suggest that benthic storage is a more realistic option than storage in the dead zone volume to explain the origin of flow-pulse biomass.

The contrasting responses of the biomass of the phytoplankton groups led us to the hypothesis that chlorophytes were predominantly planktonic, diatoms were primarily meroplanktonic, and cyanobacteria were tightly attached to the surfaces of inorganic particles. Indeed, a synthetic flow pulse in a hypothetical channel generated biomass patterns that resembled the observed responses when numerically solving Eqs. 1 and 2 with a constant $B_{p,in}$ (Fig. 5). Given the poor light climate of the rivers, however, the hypothesis of benthic retention remains tenuous without proving that meroplankty may provide an advantage under the particular set of light conditions specific to each river.

Feasibility of the benthic retention hypothesis—The density functions of both normalized flow ($\overline{Q/Q_{max}}$) and bottom light index ($\overline{K_d \times Z/2}$) were strongly skewed towards low values in each river (Fig. 6). The median value of I_z was 31%, 15%, and 6% of I^* in the Hernád, Berettyó, and Szamos Rivers, respectively (Table 3). Light conditions quickly deteriorated with increasing flow at the bottom compared to conditions in the water column (Fig. 6C).

When the bottom light index exceeded an approximate threshold of 5, even an entrained, low-light–adapted ($K_I = 20$ μmol quanta m^{-2} s^{-1}) alga was no longer able to sustain a sufficiently high growth rate to offset daily maintenance costs represented numerically by $r = 0.1$ (Fig. 7). The frequency of days with no net growth [$\overline{(f(I^*)-r)} < 0$] was relatively low in the Hernád River (about 10%) but was as high as 40% in the Szamos River. This situation prevailed when normalized flow exceeded 0.05–0.15 in the various rivers (Fig. 6C). Expressed in absolute terms, the threshold
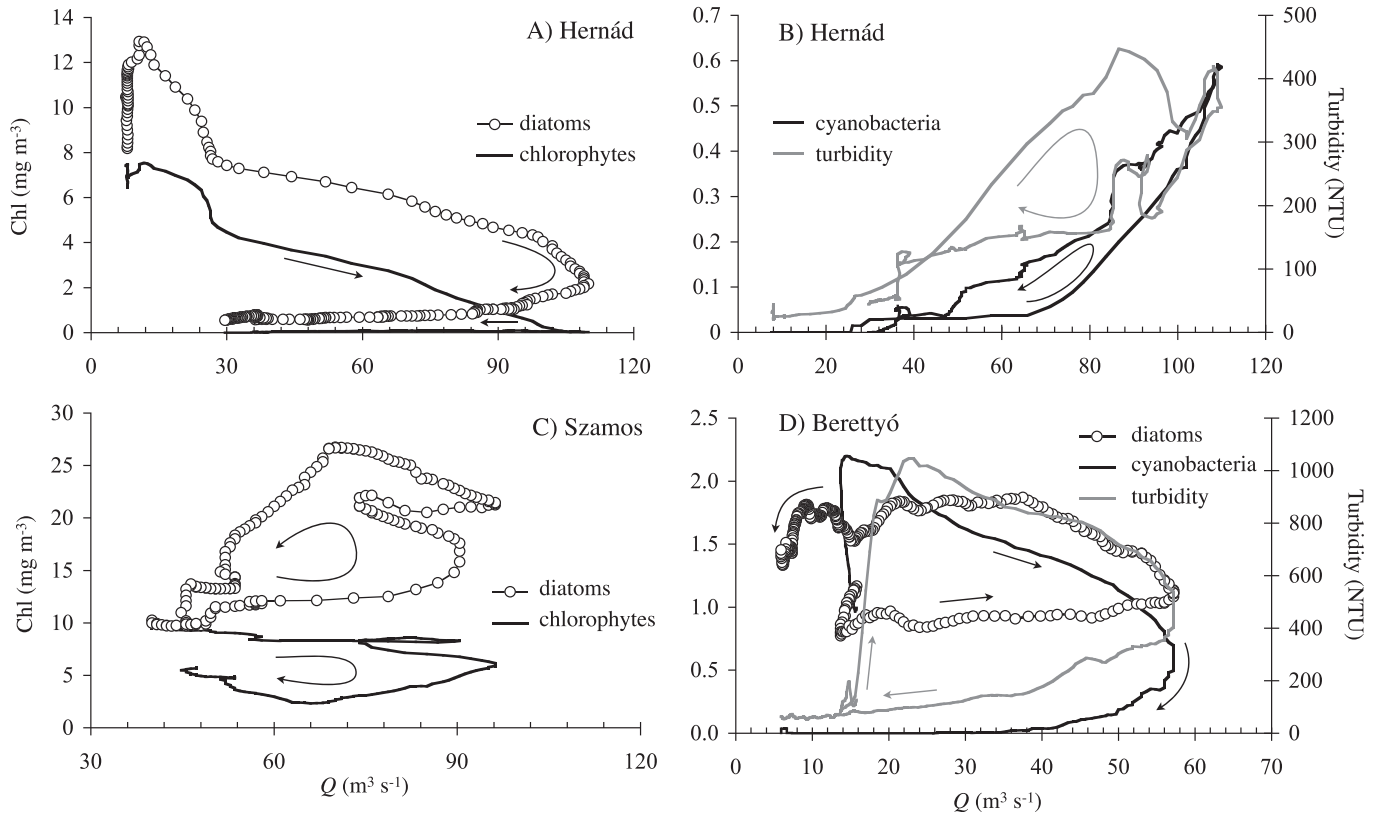
Fig. 4. Examples demonstrating the relationship between flow pulses and fluorometric Chl associated with various phytoplankton groups at an hourly scale. (A, B) Hernád River, 03–15 September 2007; (C) Szamos River, 06–13 August 2009; (D) Berettyó River, 16–31 July 2005. Arrows indicate the trajectory of biomass and turbidity pulses. (A) Except for the largest flow pulses, (C, D) the biomass of diatoms increased with increasing flow. (A, C) Chlorophytes were usually diluted; (B, D) cyanobacteria followed resuspension events with some hysteresis.

flow, above which no net growth could be maintained in the water (except with $K_I < 20$ μmol quanta m^{-2} s^{-1}) was 9, 60, and 115 m^3 s^{-1} in the Berettyó, Hernád, and Szamos Rivers, respectively (Fig. 2).
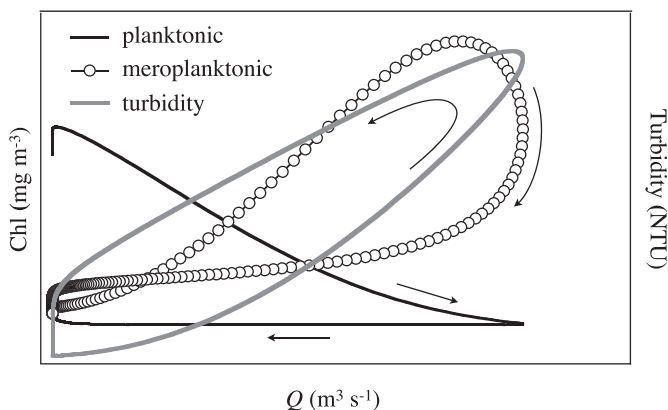

Fig. 5. The contrasting passage patterns of turbidity, a planktonic and a meroplanktonic alga during a synthetic flow pulse in a hypothetical channel. Arrows indicate the trajectory of biomass and turbidity pulses. The simple growth models were solved numerically assuming constant downstream inoculation.

When $\overline{K_d \times Z/2}$ was within a range of about 3 and 5, low-light–adapted algae might maintain a positive net growth rate in the water but not on the bottom $[\overline{(f(I^*)-r)}>0$ and $\overline{(f(I_Z)-r)}<0]$. The frequency of such days was fairly similar at the study sites (15% in the Hernád and 20% in the other two rivers; Fig. 7). The corresponding threshold for Q was around 30–35% lower than the value above which net growth ceased in the water column.

In the remaining cases net growth was possible at the bottom and thus, Eq. 9b could be used to estimate the highest $\tau_w : \tau_b$ ratio (the lowest τ_b value) that compensated for diminished bottom light exposure (Fig. 7). Ratios were as low as 0.002, i.e., $\tau_b = 500\ \tau_w$. We considered that cases with $\tau_w : \tau_b \leq 0.2$ rather than 0.002 better represented days when benthic retention might not compensate for the lower light (Fig. 7). Applying this limit and discounting cases when the Szamos River did not support net growth, our model indicated that algae might take the advantage of meroplankty as opposed to full water column entrainment for 66% of the time (Fig. 7; Table 4), provided that benthic retention time exceeded water retention time by a median factor of 1.3. Using similar reasoning, meroplanktonic algae had an advantage over planktonic algae for 67% and 80% of time in the Berettyó and Hernád Rivers. For a given τ_w value in a 1-km river length (Table 3), the compensating
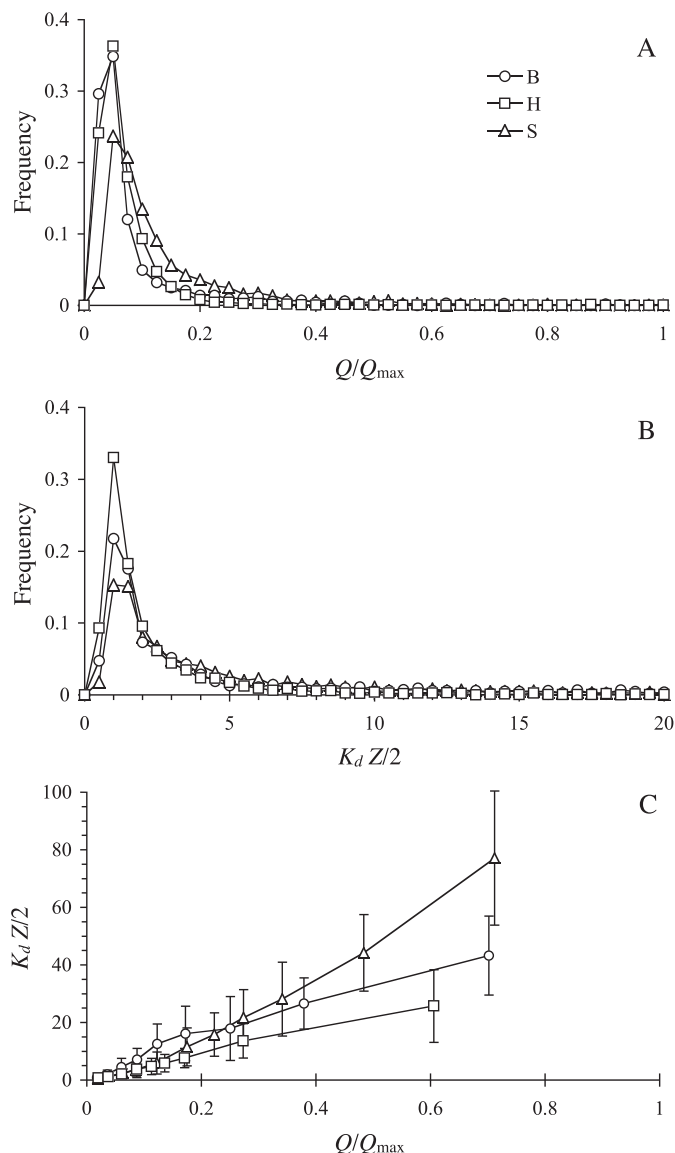
Fig. 6. Density distribution of (A) normalized flow (Q/Q_{max}), that of (B) the bottom light index ($K_dZ/2$), and (C) the relationship between the two variables. K_d is the vertical light attenuation coefficient; $K_dZ/2$ is the negative logarithm of the ratio of light exposure at the bottom and in a mixed column of depth Z. (B) The abscissa was cut down at $K_dZ/2 = 20$ to enhance visibility. B, H, S: Berettyó, Hernád, and Szamos Rivers, respectively.

median τ_b was estimated as 0.6 h (range 0.4–17), 1 h (range 0.8–4), and 0.5 h (range 0.4–1.7) in the Szamos, Berettyó, and Hernád Rivers, respectively. The corresponding median k_{resusp} equaled 3.6, 4.1, and 2.1 s m^{-2}.

A substantial population increase requires an appreciable period of time with favorable growth conditions. Random gaps in the turbidity time series prevented us from directly estimating the duration of favorable conditions when continuous net growth could occur at the bottom. The approximate threshold discharges that separated various categories of net growth allowed us to derive a rough estimate from the continuous flow record (Fig. 8). In the most turbid Szamos River, the duration and

frequency of periods with no net growth were similar to those with net growth at the bottom. A comparison with the seasonal distribution of flow (Fig. 2) indicated that periods of no growth occurred more often during the spring, whereas periods favoring meroplankty were more typical of summer and autumn. In the other rivers and particularly in the Hernád River, long unbroken flow periods were available for benthic growth and seasonality was less obvious (cf. Figs. 2, 8).

Varying the fraction respired ($0.05 \leq r \leq 0.1$) within the model extended the potential regions of both net planktonic and benthic growth nearly linearly, but the shift was negligibly small (Fig. 9). A low half-saturation constant for light-limited growth had a greater influence on growth than low r. In the Hernád River, where turbidity was usually low (Table 2), even algae with high values of K_I (60 μmol quanta m^{-2} s^{-1}) were capable of net growth at the bottom in 55% of total cases and in 70% of the time when net growth was supported in the water. In contrast, in the more turbid Berettyó River net growth of algae with $K_I = 60$ μmol quanta m^{-2} s^{-1} would have occurred 60% of the time. Considering only days when the river supported net algal growth, meroplankty might have been beneficial for > 55% of time. In the highly turbid Szamos River, meroplanktonic algae had to have $K_I \leq 40$ μmol quanta m^{-2} s^{-1} to obtain a growth advantage over planktonic algae, using a criterion of > 50% of time.

Hydraulic effect on persistence—Considering both light and temperature limitation of growth, each river supported a persistent planktonic population for only 40% of time under an extremely high retention value of $\varepsilon = 0.1$ (Fig. 10). In the relatively fast-flowing Hernád River (Table 3), virtually no planktonic population could persist in the absence of refuges provided by retention zones ($\varepsilon = 1$).

A realistic estimate of ε may fall into the range, $0.6 < \varepsilon < 0.8$ (*see* Discussion). If so, the population of the low-light–adapted planktonic alga might persist in the Szamos River for not more than one-third of the time (Fig. 10). At $\varepsilon = 0.7$, the median net growth rate of persistent populations would be 0.48 d^{-1} (range 0.18–0.71 d^{-1}), but populations growing as fast as 0.2 d^{-1} could not safely escape being washed out.

Persistent planktonic populations occurred even less frequently in the other two rivers. Assuming that dead zones occupy 30% of the cross section ($\varepsilon = 0.7$), even planktonic populations growing as fast as 0.45 d^{-1} and 0.6 d^{-1} may not be able to be self-sustaining in the Berettyó and Hernád Rivers, respectively.

Discussion

Meroplankty was the simplest explanation for pulses of diatom Chl that accompanied flow pulses that exerted low to moderate dilution in each of the three rivers (Fig. 4). Supporting lines of evidence included the distinctly different temporal dynamics of diatoms, chlorophytes, and cyanobacteria, as well as the extraordinarily large spatial heterogeneity that would have been necessary to

Table 3. Median values and ranges of derived variables averaged over a day. I_Z and I^* are the PAR at the bottom and in the mixed water column, respectively.

Variable	Berettyó		Hernád		Szamos	
	Median	Range	Median	Range	Median	Range
Mean water velocity (m s^{-1})	0.40	0.31–0.79	0.80	0.59–1.18	0.71	0.46–1.34
Depth (m)	1.0	0.3–5.4	0.7	0.3–4.2	1.2	0.4–6.9
τ_w (h)*	0.70	0.35–0.90	0.35	0.24–0.50	0.39	0.21–0.60
Light attenuation coefficient (m^{-1})	3.72	1.79–36	3.60	1.28–48	4.71	0.95–44
I_Z (μmol quanta m^{-2} s^{-1})	7.5	<245	35.3	<285	1.5	<325
I^* (μmol quanta m^{-2} s^{-1})	46.0	<365	113.9	<399	23.9	<435
I_Z/I^*	0.15	<0.69	0.31	<0.77	0.06	<0.75

* In a 1-km-long section.

store the flow-pulse biomass in upstream dead zones compared to what has been observed in rivers (Reynolds and Descy 1996; Reynolds 2000). Our field experience in three shallow, braided reaches of the River Szamos, Romania, provided supplementary evidence (V. Istvánovics unpubl. data). The overwhelmingly dominant centric diatom *Thalassiosira weissflogii* sedimented rapidly along the extended shallow bottoms of this river (depth < 0.5 m). Vigorous daytime gas ebullition and foam formation were indicative of intense benthic photosynthesis following sedimentation.

Meroplankty and light availability—Depth and turbidity varied in the study rivers (Tables 2, 3; Fig. 6) in a range similar to that of rivers of comparable size (Basu and Pick 1996; Davis and Koop 2006). The inverse relation between Chl and flow, as well as Chl and turbidity (Fig. 3) suggested strong dilution and potential for light limitation of algae—a common case in higher order rivers (Vannote et al. 1980; Schmidt 1994; Reynolds and Descy 1996). Indeed, model results suggested that the two lowland rivers (the Szamos and the Berettyó) supported net growth of a low-light–adapted planktonic alga (K_I = 20 μmol quanta m^{-2} s^{-1}) only 60–70% of the time, whereas the duration when light conditions were replete for net growth was higher (some 90%) at the middle-reach monitoring site in the Hernád River (Fig. 7). Even more notable was the length of the unbroken periods (up to 3 months), during which our model indicated that algae might not grow at all in the lowland rivers (Fig. 8). Albeit the monitoring sites were situated in relatively deep sections of the channels, these findings clearly demonstrated that light is a key factor in selecting for algal species in our rivers.

In shallow lakes, where wind-induced entrainment of meroplanktonic diatoms is an important process, mean turbidity can approach (Honti et al. 2007) or even exceed (Schelske et al. 1995) that in the Szamos River. Similarly to the observations made in lakes (Carrick et al. 1993; Schelske et al. 1995), the formation of resting propagules in fluvial meroplanktonic diatoms might extend the period when meroplanktonic algae are favored in our rivers. For example, *Stephanodiscus* species that frequently dominate in rivers (Rojo et al. 1994) are known to form resting stages (Schelske et al. 1995).

Considering serious light deficiency, it might be surprising that the divide was not so much between conditions that favored meroplankty as opposed to a truly planktonic life cycle; it rather separated regions where the particular river did or did not support net phytoplankton growth. The frequency of days was similar in each river when net growth was possible in the mixed column but not on the bottom (15–20% of time; Fig. 7). In the majority of cases, such conditions prevailed for periods less than 2–3 d (Fig. 8). Consequently, a 30–40% (as a median) longer retention time in the benthos relative to that in the water might have been sufficient to compensate for slower light-supported net growth at the bottom (Fig. 7). Even though light was the primary growth-limiting factor, strategies to avoid washout determined the ultimate success of algae in rivers.

This assertion conforms to the primary paradigm of potamoplankton ecology (Reynolds and Descy 1996; Reynolds 2000) in the sense that refuges provided by retention zones play a crucial role in downstream recruitment of riverine algae. At the same time, however, we interpret sedimentation in a distinctly different way than the current paradigm, which looks upon this process simply as a loss term.

The significance of sedimentation–resuspension to meroplankty—Sedimentation has been followed in tracer release experiments in flows ranging from second-order streams to the sixth-order River Spree, Germany. The outcome of most of these studies is surprisingly similar and nontrivial (Thomas et al. 2001; Packman et al. 2003); although the fall velocity of various tracers under quiescent conditions spanned over five orders of magnitude (< 10^{-5} mm s^{-1} in < 1-μm diameter bacteria; < 1 mm s^{-1} in <200 μm organic seston), the deposition velocity varied relatively little (from 0.1 to 1 mm s^{-1}). The authors concluded that gravitational forces dominated deposition of > 100-μm diameter particles, whereas local hydrological and benthic conditions set the minimum rate of deposition for < 100-μm particles that settled more rapidly than their fall velocities in quiescent water. This conclusion was confirmed theoretically by a stochastic diffusion model of particle transport (McNair 2006). The model conformed well to field observations under the assumption that only a fraction of particles that hit the bottom actually settled permanently. Turbulence ensured fast delivery of particles to the interface, and thus, hyporheic exchange with the permeable streambed determined the rate of deposition. Filtering out of fine particles by the inorganic sediment
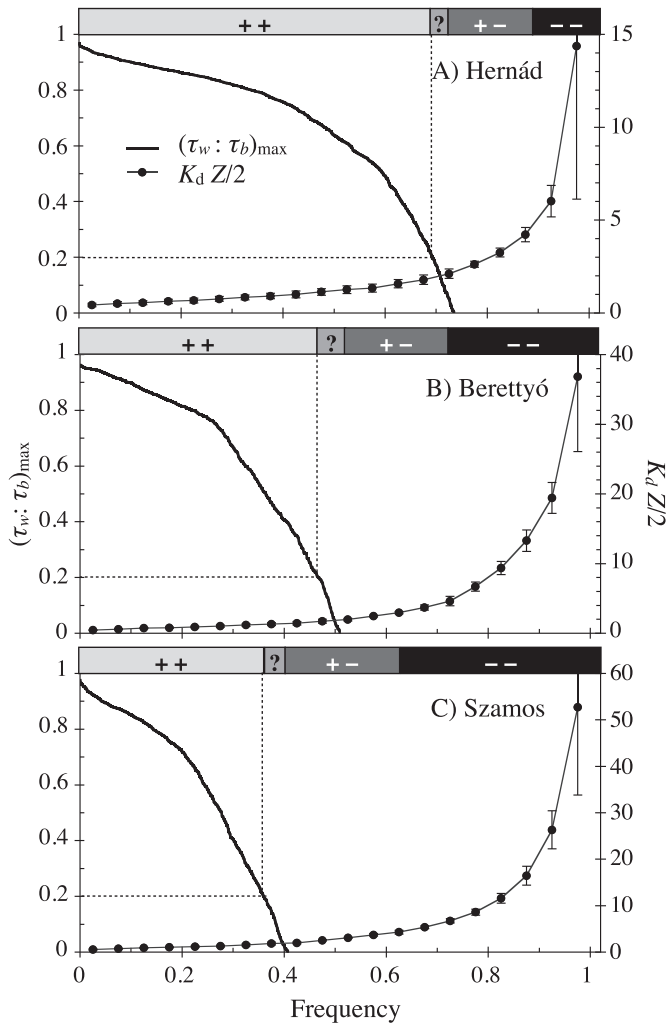
Fig. 7. Cumulative frequency distribution of the highest $\tau_w : \tau_b$ ratio (the shortest benthic retention time) compensating for the lower light exposure at the bottom relative to that in the mixed column in (A) Hernád, (B) Berettyó, and (C) Szamos Rivers. The corresponding values of the bottom light index, $K_d Z/2$, were averaged in frequency steps of 0.025. Calculations were performed for an alga with $K_I = 20\ \mu$mol quanta m^{-2} s^{-1}, $r = 0.1$. Regions with minus and plus signs denote days when net growth rate in the mixed column (G_p) and at the bottom (G_b) was as follows: $G_p < 0$ and $G_b < 0$ (net growth is impossible); $G_p > 0$ and $G_b < 0$ (net growth is possible only in the water); $G_p > 0$ and $G_b > 0$ (net growth is possible at the bottom), respectively. In the latter region, meroplankty is beneficial. Question mark indicates the region where $G_b > 0$ but the compensating $\tau_w : \tau_b$ ratio was assumed to be unrealistically low.

matrix or trapping by biofilms enhanced deposition (Packman et al. 2003). This theoretical and observational reasoning led us to consider that the deposition model of Thomas et al. (2001) was applicable to our rivers, even though in the largest river where sedimentation has been experimentally investigated (the Spree River), fall and deposition velocities seemed to be almost identical (Wanner and Pusch 2000).

This model of fine particle deposition is highly relevant for the settling behavior of riverine phytoplankton repre-

Table 4. Frequency of categories of net growth. n, number of days analyzed; G_p and G_b, net growth rate in the mixed column and at the bottom, respectively. When $G_p > 0$ and $G_b > 0$, meroplankty is beneficial. Calculations were performed for an alga with $K_I = 20\ \mu$mol quanta m^{-2} s^{-1}, $r = 0.1$.

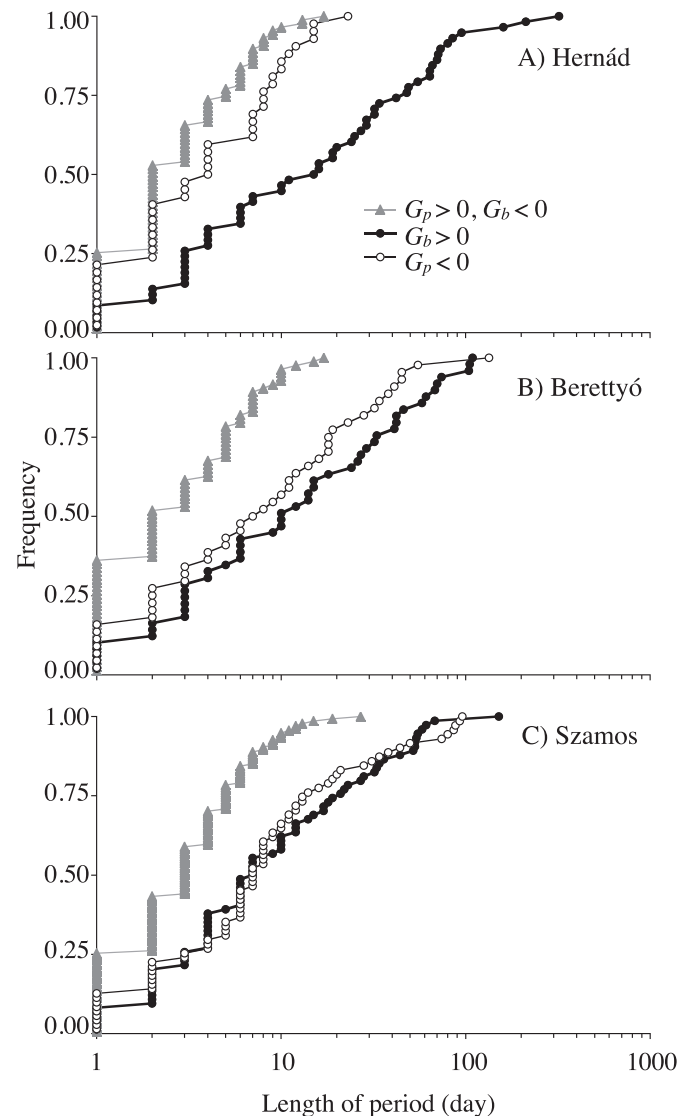| River	n	Frequency of growth categories		
		$G_p<0$, $G_b<0$	$G_p>0$, $G_b<0$	$G_p>0$, $G_b>0$
Szamos	2033	0.38	0.21	0.41
Berettyó	1532	0.30	0.23	0.47
Hernád	2360	0.12	0.18	0.70

Fig. 8. Cumulative frequency distribution of the length of unbroken periods when net growth was possible at the bottom ($G_b > 0$) and only in the water ($G_p > 0$, $G_b < 0$), and when no net growth occurred ($G_p < 0$). (A) Hernád River, (B) Berettyó River, (C) Szamos River. Calculation is based on flow thresholds estimated for an alga with $K_I = 20\ \mu$mol quanta m^{-2} s^{-1} and $r = 0.1$ (see Fig. 2). When $G_b > 0$, meroplankty provides an advantage.
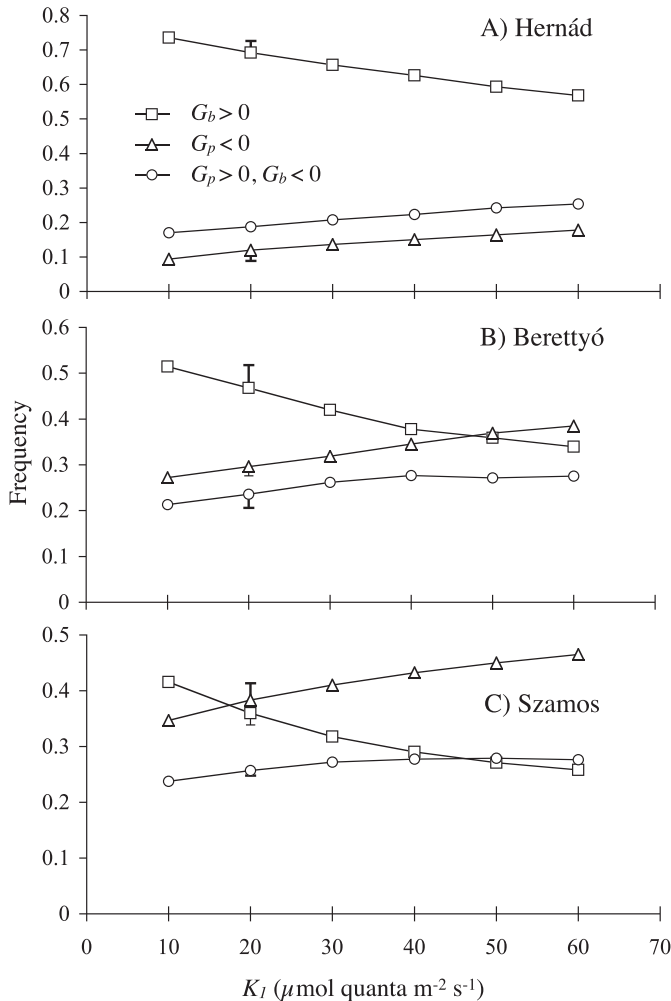
Fig. 9. Frequency of days as a function of the half-saturation constant of light (K_I) when phytoplankton could maintain a positive net growth at the bottom ($G_b > 0$), only in the water ($G_p > 0$, $G_b < 0$), and net growth was unsupported by light availability ($G_p < 0$) in (A) Hernád, (B) Berettyó, and (C) Szamos Rivers. The respired fraction was $r = 0.1$. Vertical bars at $K_I = 20$ μmol quanta m^{-2} s^{-1} indicate the shift caused by a lower r of 0.05.
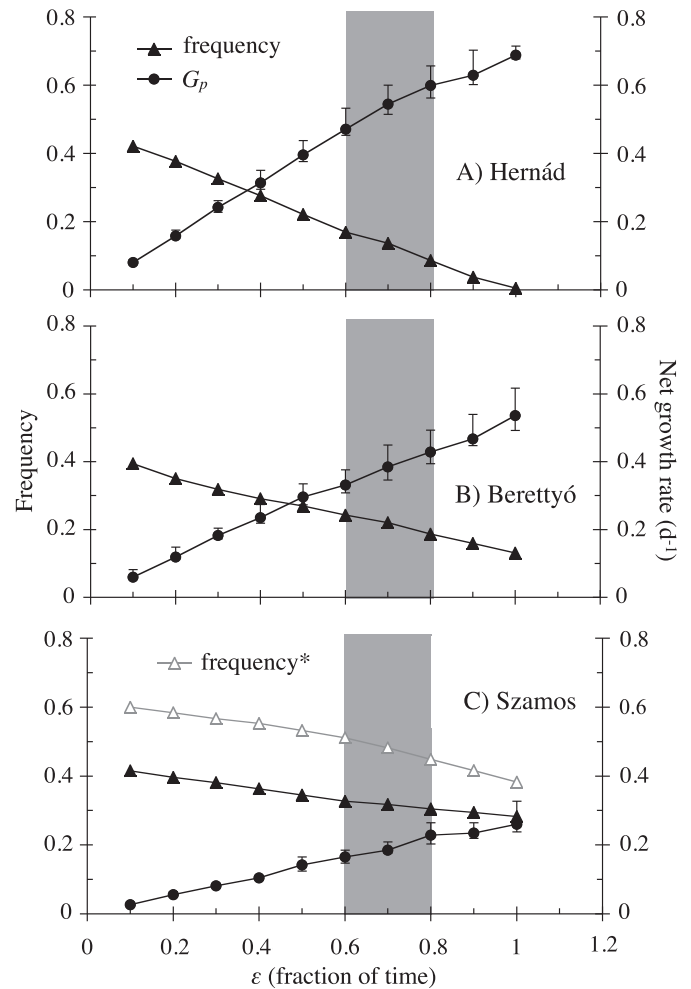

Fig. 10. Frequency of days as a function of time spent in the bulk flow (ε) when (A) Hernád, (B) Berettyó, and (C) Szamos Rivers supported persistent planktonic population of a low-light–adapted test alga and the overlapping range of net growth rates (G_p) when both persistent and nonpersistent populations could be observed. Calculations were performed for an alga with $K_I = 20$ μmol quanta m^{-2} s^{-1}, $r = 0.1$. In the case of growth rates, the symbol is the median, and bars indicate minimum and maximum values. In the Szamos River, frequency of persistent days was also calculated by neglecting temperature dependence of growth (frequency*). The grey region is the likely range of ε.

sented by small (< 100 μm), fast-growing, opportunistic species (Emiliani 1997; Reynolds 2000; Chételat et al. 2006). It implies that traits that efficiently diminish sedimentation losses in deep lakes (Reynolds 1997) may not help to escape rapid deposition in turbulent rivers. We propose that in rivers, meroplankty is a specific adaptation that allows these algae to take the advantage of a naturally fast sedimentation rate by reducing the exposure to flushing.

Our data allow us to estimate the minimum benthic retention time needed to compensate for the inferior light availability at the bottom (Fig. 7). As opposed to lakes (Luettich et al. 1990; Hamilton and Mitchell 1996; Koski-Vähälä and Hartikainen 2001), resuspension has received little attention in running waters. In the River Spree, an experimental flow pulse (nearly twofold increase in Q from 7.9 m^3 s^{-1}) was observed to resuspend 10% of settled

Lycopodium spores in 9 h (Wanner and Pusch 2000). In a second-order stream in Idaho, 98% of the deposited particles were resuspended within 1 d (Cushing et al. 1993). In another small stream, organic seston (15–52 μm) showed biphasic resuspension kinetics under stable flow conditions. Mean benthic residence time was 13 h and 7.5 d for one-third and for the remainder of the seston tracer, respectively (Newbold et al. 2005). These data suggested that the rate of resuspension is highly site specific. Our estimates of compensating τ_b to offset lower bottom light relative to the water column were at the lower end of the observed range.

Considering only the high rate of flushing (Table 3) and the relatively long periods when sufficient light was available at the bottom to sustain net growth (Fig. 8),

one might assume that the longer benthic residence would support higher biomass of meroplanktonic species. However, continuous resuspension and sedimentation of inorganic particles may bury the settled algae, thereby offsetting the benefits of a long benthic residence, while, additionally, probability of consumption by benthic invertebrates would increase. Obligate and facultative deposit feeders (chironomids, unionids, gastropods) are generally abundant in large lowland rivers (Gosselain et al. 1994; Reynolds and Descy 1996), including our study rivers (Sárkány-Kiss and Hamar 1999; Vaughn and Hakenkamp 2001; Cupşa et al. 2009). Further studies on the roles of both resuspension and benthic grazing are needed under various flow regimes to evaluate the benefits of the proposed benthic retention mechanism.

Persistence of planktonic and meroplanktonic populations—We support the argument by Reynolds and Descy (1996) that inoculation is probably the most challenging unresolved problem in fluvial phytoplankton ecology and that inoculation from backwaters and side arms is, at best, an incomplete explanation. At the same time, however, we argue that the magnitude of the inoculation problem goes far beyond the case of slowly growing populations, and thus a seasonal process (overwintering of resting stages) does not bring us closer to the solution. We illustrate this with the following examples.

(1) In a modeling study, Honti et al. (2010) showed that 10% of the Chl flux at the outflow of the Zala River (drainage area is 1528 km², $L = 100$ km, $Q = 4$ m³ s⁻¹) represented the necessary inoculation to support the prevailing algal biomass through the entire fluvial network where τ_w extended to nearly 2 weeks because of a number of small reservoirs. Without reservoirs, τ_w was estimated to drop to one-tenth of the present value. At this short residence time, over two-thirds of the outflowing Chl originated directly from inoculation as opposed to growth along the fluvial network.

(2) Let us make a simple thought experiment. We assume that net growth in the dead zones is sufficiently high to sustain a persistent planktonic population downstream, so no additional sources of inoculation (backwaters, reservoirs, etc.) are needed. At $t = 0$, growth conditions deteriorate in such a way that net growth drops to exactly zero in the dead zones. From this moment onward, dead zone algae behave like a conservative material. Let Q_{ex} (m³ s⁻¹) denote the exchange flux between the bulk flow and the dead zone volume (V_{dz}, m³). The water retention time in the dead zone is $\tau_{dz} = V_{dz}/Q_{ex}$. Because there is no inoculation from the upstream section, a simple first-order dilution equation describes the temporal change in dead zone biomass, $B_t = B_0 \exp(-t/\tau_{dz})$. Unbroken periods, during which light did not support net growth in the water, lasted 4 and 7 d or longer in half of the cases in the Hernád River and in the other two rivers, respectively (Fig. 8). Assuming a τ_{dz} value of 2 h (Engelhardt et al. 2004), the exponent, t/τ_{dz}, becomes 48 and 84 for each case, respectively. The resulting $B_t : B_0$ ratio (in the order of 10^{-21} and 10^{-37}, respectively) indicates that even very large populations of planktonic alga would be washed out from the dead zone. Assuming realistic cell numbers, adverse growth conditions for a period of only 20–30 τ_{dz} ($B_t : B_0$ is $<10^{-9}$ to $<10^{-13}$) will fully eliminate the inoculation capacity of any water parcel in a continuous exchange with the bulk flow.

(3) The criterion of Speirs and Gurney (2001) indicated that conditions allowing the persistence of planktonic algae could be considered rare in our rivers (Fig. 10). The ADZ model of Davis and Atkinson (2000), which derives longitudinal dispersion entirely from ADZ storage, helps to estimate the likely range of time spent in the dead zones with no advection (ε in Eq. 10). According to the ADZ model, the net downstream migration velocity of a particle is $v \times \chi^2/(1 + \chi^2)$, where the storage parameter, χ^2, is the ratio of the cross-sectional area of the bulk flow region (A_{bf}, m²) to the dead zone area (A_{dz}, m²). Inserting this formula into the persistence criterion of planktonic populations (Eq. 10), $\varepsilon = \chi^2/(1 + \chi^2)$ and thus, $A_{dz}/(A_{dz} + A_{bf}) = 1 - \varepsilon$. Reynolds (2000) observed that dead zones occupy 20–40% of the cross-sectional area in many rivers ($0.6 < \varepsilon < 0.8$). For this retention, even high net growth rates would not always guarantee persistence (Fig. 10). Stochasticity of flow appears to be the reason that even vigorously growing planktonic populations may be washed out except in extremely dry years (cf. Fig. 2).

To quantify the difference in self-sustaining capacity of meroplanktonic and planktonic populations, an estimate for ε is also required for meroplankton. Although a compensating local benthic residence time could be estimated relative to τ_w (Eq. 9b and Fig. 7), the unknown rate of resuspension prevented the extension of this approach to the whole upstream section of the river. Nevertheless, it is evident that meroplanktonic species will be persistent more often under the same flow conditions than their planktonic counterparts.

Obviously, maintaining persistence is an everyday challenge even for fast-growing populations of planktonic algae. Therefore we propose that self-sustaining phytoplankton populations in large, turbid rivers are meroplanktonic. An equivalent proposition is that truly planktonic populations are necessarily dependent on periodic inoculations from out-of-channel sources. Thus there is a common pattern that primarily planktonic chlorophytes are the most species-rich group in rivers, whereas a few (meroplanktonic) diatom species dominate the biomass (Rojo et al. 1994; Reynolds and Descy 1996).

Generalization of the benthic retention hypothesis—Walks (2007) examined persistence of planktonic populations by using the criterion of Speirs and Gurney (2001) for a wide selection of flowing waters, in which τ_w spanned over four orders of magnitude. He estimated that in most streams and rivers, populations of both phyto- and zooplankton should spend less than 30% of time in the bulk flow to persist ($\varepsilon \leq 0.3$). Despite the large uncertainty of water residence time in his study, the unrealistically high dead zone ratio ($1 - \varepsilon \geq 0.7$) indirectly supported our benthic retention hypothesis and suggested that meroplankty might be a general prerequisite for persistence of phytoplankton populations. By analogy, we suggest that zooplankton may

require behavioral, meroplanktonic, or other types of life history adaptations to benefit from the presence of flow refugia (Reckendorfer et al. 1999; Schiemer et al. 2001).

The proposed benthic retention mechanism certainly has its physical limits. Meroplankty loses its feasibility in deep and turbid channels where no light penetrates to the bottom (Sellers and Bukaveckas 2003; Istvánovics et al. 2010). Many studies have observed that net production and biomass of phytoplankton peak in flows of intermediate stream order (Vannote et al. 1980; Billen et al. 1994). An analogous pattern is also characteristic of the downstream reaches of large rivers (Dokulil 1994; Reynolds and Descy 1996; Honti et al. 2008). It is, however, interesting to note that in the Danube River the decrease in biomass and net production downstream of the Iron Gate (river km ~1700; Serbia) was followed by a conspicuous increase from about Nikopol, Bulgaria (river km ~600; Dokulil 2006). The latter reach was the one where Stoyneva (1994) observed the significant role of shallow areas in phytoplankton recruitment. Thus, benthic retention and meroplankty may better be predicted from channel depth than river size (cf. Figs. 7, 8, 10; Stoyneva 1994).

The benthic retention hypothesis is relevant to medium and large rivers, which are sufficiently shallow during a part of the growing season for some light to penetrate to the bottom. In such flows, meroplanktonic algae have the advantage of a prolonged benthic residence relative to water residence time. Recolonization of the water column critically depends on the nearly unknown rate of resuspension. Whereas persistence of planktonic populations requires periodic inoculations from out-of-channel sources, self-sustaining riverine algae are meroplanktonic. Chlorophytes and diatoms are the prominent representatives of the former and the latter groups, respectively.

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