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Distribution of macroinvertebrates in relation to the quantity and quality of organic matter in streams in the western Czech Republic

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Abstract

Data on benthic macroinvertebrates from the western Czech Republic were used to test the hypothesis that benthic macroinvertebrates are either ‘low-cost’ or ‘high-cost’ life forms. A wide head and long legs were regarded as ‘high-cost’ features, whereas a simple tube-like body without appendages as ‘low-cost’. A second hypothesis was that the quantity and nutritional value of benthic and suspended organic matter ingested was correlated to the forms present. The suspended organic matter deposits on the bottom, so total organic carbon concentration (TOC) was used to represent food availability. Because the nutritional value depends on the quantity of algae, the chlorophyll-a concentration to TOC ratio (Chl-a : TOC) was used to represent food quality. The results confirmed both hypotheses, showing that the high-cost life forms prefer high food quality (Chl-a : TOC) and low food quantity (TOC), whereas the low-cost life forms prefer the opposite. The findings help to better understand the distribution patterns of rare and endangered species.

Key words: total organic carbon, chlorophyll-a, food.

1. Introduction

Organisms can allocate energy and nutrients in various ways. The growth of a body part can be increased at the expense of another part. For instance, in case of some insect species, flightless morph females with reduced flight muscles show an increased fecundity (Chown, Nicolson 2004) due to the altered allocation of nutrients. The reduction of unused body compartments may either increase the fecundity of aquatic macroinvertebrates or, it may preserve fecundity if the nutritional quality of food is poor. Morphological traits such as body size (Usseglio-Polatera *et al.* 2000) may thus reflect environmental conditions. For example, the body size and the area of the base of the thoracic horn are good predictors of oxygen tolerance in the Chironomini tribe of Chironomidae (Rossaro *et al.* 2007). Benthic macroinvertebrate life forms may be regarded as high-cost, if they need energy and nutrients to build structures that the low-cost life forms don’t build. In the case of Plecoptera and Ephemeroptera, such structures may include especially a wide head and long legs. These features enable them to collect or find food more effectively, or escape predators. However, if the food is abundant or low quality, such features are not necessary or affordable and low-cost life forms are preferred.

The nutritional quality of organic matter as food in streams may be influenced by the quality of suspended matter, particularly if the food is collected in lower current speed areas, where suspended matter deposits. During decomposition of coarse particulate organic matter in streams, the content of the refractory compounds increases (Cummins, Klug 1979; Peters *et al.* 1989) and nutritional quality decreases. For example, Ward and Cummins (1979) found that the chironomid *Paratendipes albimanus* (Meigen, 1818) fed with natural detritus, exhibited much lower growth rates than if fed with colonized leaf fragments. In contrast, algal periphytes are food of high nutritional value: assimilation efficiencies of invertebrate grazers are high compared to their low assimilation efficiencies on detritus (Cummins, Klug 1979; Hornick *et al.* 1981; Pandian, Marian 1986; Allan, Castillo 2007). Thus, the nutritional value of suspended matter in streams may correlate with algal (phytoplankton) content. According to Reynolds (1984), the normal carbon content of algal cells is 51-56% and the content of chlorophyll-a is 0.9-3.9 % of their ash-free dry weight. Consequently, the carbon to chlorophyll-a ratio in dry mass is approximately 25. This ratio of 25 was also measured by Admiraal *et al.* (1992) in the lower Rhine. If the chlorophyll-a concentration is 20 μg dm^{-3}, the corresponding algal carbon concentration is approximately 0.5 mg dm^{-3}. Then, if the particulate organic carbon concentration is 2 mg dm^{-3}, the algae account for about one quarter of the particulate matter. Therefore, the algae content can be high enough to enhance the nutritional value of the particulate matter significantly.

Deposited particulate matter can be resuspended again; Newbold *et al.* (2005) found in a mountain stream that fine particulate organic matter resuspended after a residence time of 2.2 days and that very fine particulate organic matter resuspended after a residence time of 5.1 days. Ock and Takemon (2010) found by tracing lentic plankton from dam reservoirs, that fine particulate matter decreased exponentially in rivers and canals downstream. Diatom emigration into drift and immigration onto substrate may constitute substantial proportions of benthic diatom abundances (Stevenson, Peterson 1991). The immigration rates are greater in areas sheltered from current (Stevenson 1983). Roeder (1977) found positive linear relationship between the proportion of diatoms *Nitzschia acicularis* (Kützing) W. Smith, 1853 and *Nitzschia* Hassall, 1845 spp. in the plankton and epipelon. Planktonic centric diatoms *Stephanodiscus* Ehrenberg, 1846 and *Cyclostephanos* Theriot *et al.*, 1987 may also be abundant in periphyton when abundant in plankton (Werner, Köhler 2005). So, the composition of the suspended and the benthic particulate organic matter may be correlated; indeed this may be valid generally, not only downstream of reservoirs. In addition, detritus may be the dominant material ingested by scrapers such as *Rhithrogena* Eaton, 1881 and *Epeorus* Eaton, 1881 of the family Heptageniidae (Minshall 1967; Hamilton, Clifford 1983). Diatom consumption is sometimes elevated in spring and autumn (Hamilton, Clifford 1983); Coffman *et al.* (1971) found mayflies to ingest dominantly algal food in the autumn in a woodland stream. Not only does the quality of particulate matter probably affect the quality of the benthic matter, but also dissolved organic matter is important, as it is assimilated into microbial biomass (Allan, Castillo 2007).

This paper addresses the question of whether the amount and composition of organic matter in streams influences the distribution of morphological adaptations of aquatic insects. It tests two hypotheses, using data from the western part of the Czech Republic. The first hypothesis is that benthic macroinvertebrates are either ‘low-cost’ or ‘high-cost’ life forms. A second hypothesis was that the quantity and nutritional value of benthic and suspended organic matter ingested was correlated to the forms present.

2. Material and methods

All streams studied are part of the Labe (Elbe) river system in the western part of the Czech Republic (Fig. 1). The Vltava River is the largest of them. The macroinvertebrate distribution and water chemistry data were collected by staff of Povodí Ohře, s.p. (Ohře River Authority) in 2005-2007, and Povodí Vltavy, s. p. (Vltava River Authority) in 2005-2009 (in 2005 only chemistry). Most data on the macroinvertebrates were collected or revised by the author. A record of the rare stonefly *Brachyptera braueri* (Klapálek, 1900) from one site was added (Bojková, Špaček 2006; Skála, pers. obs. 2010). The data on chemistry in 2005-2008 are available online in the ARROW (2010) information system. Streamflow data are from Kestřánek *et al.* (1984), or from FFS (2010). Data on Strahler order of the streams are from HEIS WRI (2010). The macroinvertebrate samples were taken within one to four years and the water samples within one to five years in the period 2005-2009. From all available data, only 67 sampling sites were used, where mayflies of the family Heptageniidae were present. Thus, polluted streams and streams with unsuitable substrate were not taken into account. The mean environmental characteristics are presented in Table I.

During each year’s sampling period, water samples were taken monthly. Total organic carbon

(TOC) and dissolved organic carbon (DOC) were determined using high temperature catalytic oxidation with infrared detection of the CO_2 liberated. Particulate organic carbon (POC) concentration was calculated as the difference between TOC and DOC concentrations. Chlorophyll-a was determined spectrophotometrically after extraction in ethanol. Absorption was measured at 665 nm and 750 nm. The latter value was subtracted from the first to correct for turbidity. Chlorophyll-a concentration was calculated by

$$Chla = \frac{(A - A_a)}{K_c} \cdot \frac{R}{R-1} \cdot \frac{10^3 V_e}{V_s d}$$

where A is absorption before acidification, A_a absorption after acidification, K_c = 82 dm^3 μg^{-1} cm^{-1} is absorpt ion coefficient, R = 1.7 is A/A_a ratio of

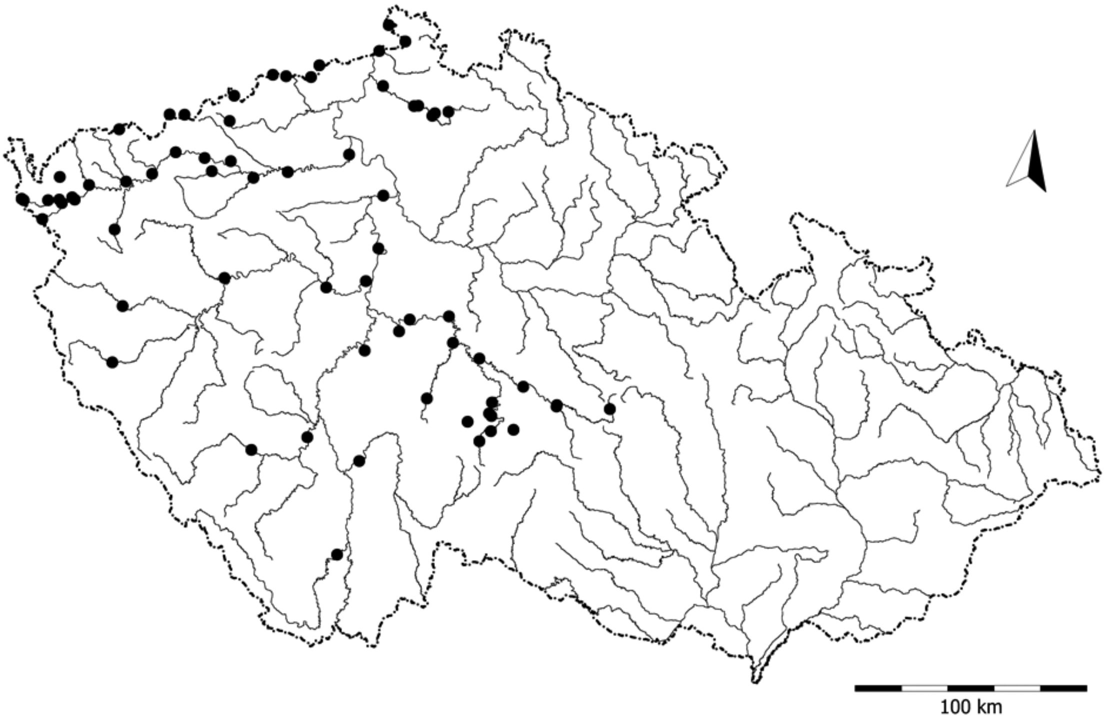

Fig. 1. Map of the Czech Republic with the sampling sites.

Table I. The environmental characteristics of the study sites. Abbreviations: TOC – total organic carbon, Chl-a – chlorophyll-a, Chl-a : TOC – chlorophyll-a to total organic carbon ratio, BOD_5 – five-day biochemical oxygen demand, POC – particulate organic carbon, TP – total phosphorus. [a]Data on BOD_5, POC, and oxygen saturation were only available from 66, 54, and 63 sites, respectively.

	Mean	Median	Minimum	Maximum
TOC (mg dm^{-3})	7.3	7.3	2.8	13.1
Chl-a (µg dm^{-3})	13.3	9.9	0.5	65.6
Chl-a : TOC (µg dm^{-3} : mg dm^{-3})	1.6	1.2	0.1	6.3
[a]BOD_5 (mg dm^{-3})	2.3	2.3	0.8	5.2
[a]POC (mg dm^{-3})	1.7	1.6	0.4	4.3
streamflow (m^3 s^{-1})	12	1.9	0.2	151
altitude (m)	377.2	385	124	738
Strahler order	5	5	3	8
water temperature (°C)	9.6	9.7	7.3	12.3
oxygen (mg dm^{-3})	10.8	10.9	9.3	11.7
[a]oxygen saturation (%)	97.2	97.9	82.2	107
pH	7.5	7.5	6.6	8.4
conductivity at 25 °C (mS m^{-1})	29	28.2	6.3	77.2
TP (mg dm^{-3})	0.092	0.076	0.01	0.316

pure chlorophyll-a, V_e – volume of extract in cm^3, V_s – volume of filtered water in dm^3, d – length of light path in cm (Dalešický *et al.* 1996). Macroinvertebrate samples were collected by a hand net with 500 μm mesh size twice a year, generally in spring and autumn, but in 2006, often in the summer. The net was placed on the bottom and the bottom was disturbed close upstream (kick sampling). The sampling and processing method partly changed. In 2005, the monitoring was focused on the assessment of organic pollution, according to the saprobic system (Sládečková *et al.* 1998; Rolauffs *et al.* 2004). Stony places in midstream were preferred for sampling. Organisms were picked out from the sample at the sampling site in sufficient quantity for their identification. The abundances of organisms were estimated and coded as integer numbers according to a logarithmic scale. In the years 2006-2009, sampling was carried out according to the multi-habitat semi-quantitative sampling technique PERLA (Kokeš *et al.* 2006). During the three-minute-long sampling, all habitats were sampled in proportion to their area within the sampling section. All organisms from a quarter or more of the sample were picked out, identified, and counted. Identification followed keys by Raušer (1980), Waringer, Graf (1997), Haybach (1999), Bauernfeind, Humpesch (2001), Haybach, Belfiore (2003), Kłonowska-Olejnik (2004), Zwick (2004), Eiseler, Haybach (2006). Late instars were identified to the level of species.

Principal component analyses (PCA) of data were performed using PAST software version 1.94b (Hammer *et al.* 2001).

3. Results

The ordination diagram based on PCA of the environmental characteristics (Fig. 2) indicates that total organic carbon (TOC) and chlorophyll-a to TOC (Chl-a : TOC) ratio (the ratio of the mean values) are strongly correlated with each other but little correlated with altitude, Strahler stream order, streamflow or water temperature. TOC is less correlated with Chl-a : TOC than with Chl-a.

PCA analysis (Fig. 3) based on the morphological characters of Heptageniidae, Leptophlebiidae, Potamanthidae (Ephemeroptera) and Taeniopterygidae (Plecoptera) given in Table II, led to groups of species that are similar to each other in morphological characters to be treated as single life forms. Thus, each genus of Heptageniidae (*Ecdyonurus* Eaton, 1868, *Electrogena* Zurwerra & Tomka, 1985, *Heptagenia* Walsh, 1863 and *Rhithrogena* Eaton, 1881) was considered a single life form. The genera of Taeniopterygidae *Brachyptera* Newport, 1849 and *Taeniopteryx* Pictet, 1841 were similar to each other, forming another group. *Potamanthus* Pictet, 1843 of Potamanthidae and *Paraleptophlebia* Lestage, 1917, *Habroleptoides* Schoenemund, 1929 and *Habrophlebia* Eaton, 1881 of Leptophlebiidae form one other group. *Choroterpes picteti* (Eaton 1871) of Leptophlebiidae stands alone. The morphological characters are only little correlated with the body length (Fig. 3).

An ordination diagram based on the PCA of morphological characters, Chl-a : TOC ratio and TOC is shown in Fig. 4. For each species, mean values of Chl-a : TOC ratio and TOC were calculated, based on the values from all the sites where the species was found. The values of TOC were tightly correlated with the values of Chl-a : TOC ratio (Pearson correlation coefficient r = 0.86), so TOC residuals from the linear regression analysis of both variables with TOC as dependent variable were used instead of TOC. Morphological characters were positively correlated with Chl-a : TOC ratio and negatively correlated with TOC residuals in the ordination diagram. Chl-a : TOC ratio was more correlated with the length of femora than with characters related to the width of the fore body. On the contrary, TOC residuals were more negatively correlated with the characters related to the width of the fore body. *Epeorus assimilis* Eaton, 1885 was excluded from the analysis as the most rheophile species, having immovable gills (Bäumer *et al.* 2000) with friction pads (Ditsche-Kuru, Koop 2009). *Potamanthus*, *Paraleptophlebia* and *Habroleptoides* were excluded as the least rheophile genera. If included, the analysis yielded a similar diagram. However, Chl-a : TOC ratio was more correlated with TOC residuals and less correlated with morphological characters and all the morphological characters were more corre-

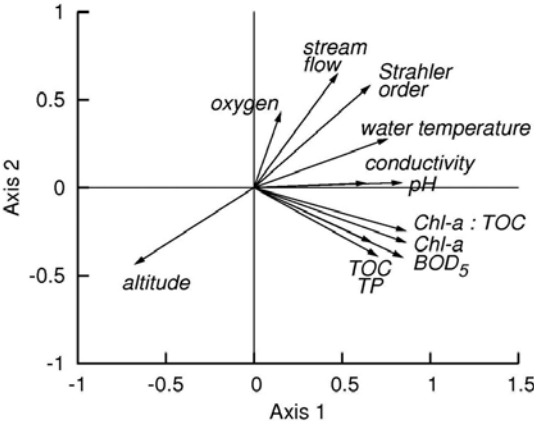

Fig. 2. Correlation biplot based on principal component analysis (PCA) of the environmental variables at 66 sampling sites. One site was excluded from the analysis due to missing data. The axes 1 and 2 explained 49% and 15% of the variance, respectively. The abbreviations are given in Table I.

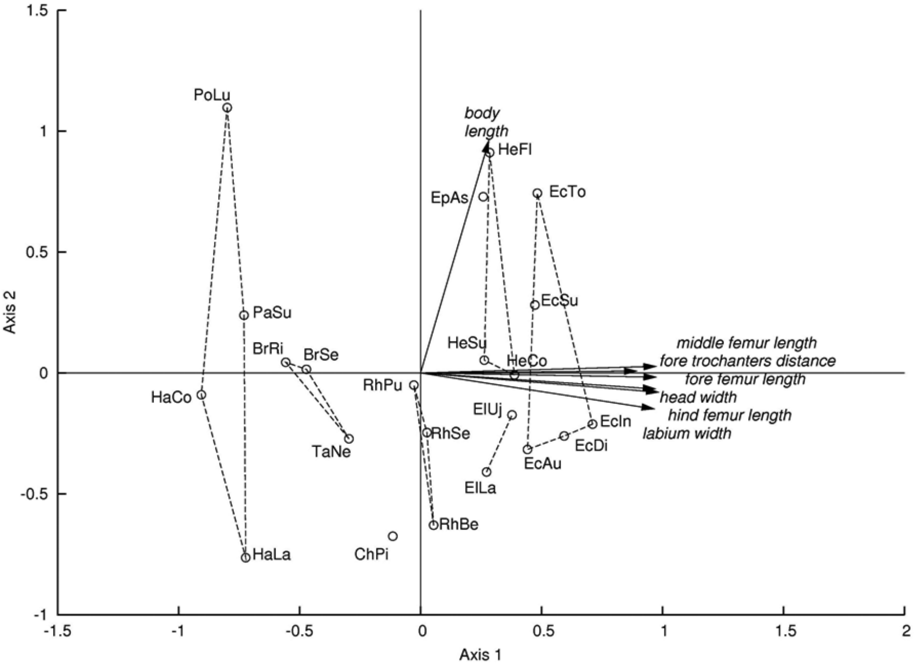

Fig. 3. Correlation biplot based on principal component analysis (PCA) of the morphological characters of aquatic insect nymphs presented in Table II. The axes 1 and 2 explained 79% and 14% of the variance, respectively. Species are grouped according to their life forms and the groups are delineated with convex hulls. The species scores (points) were multiplied by 0.5. Abbreviations in Table II.

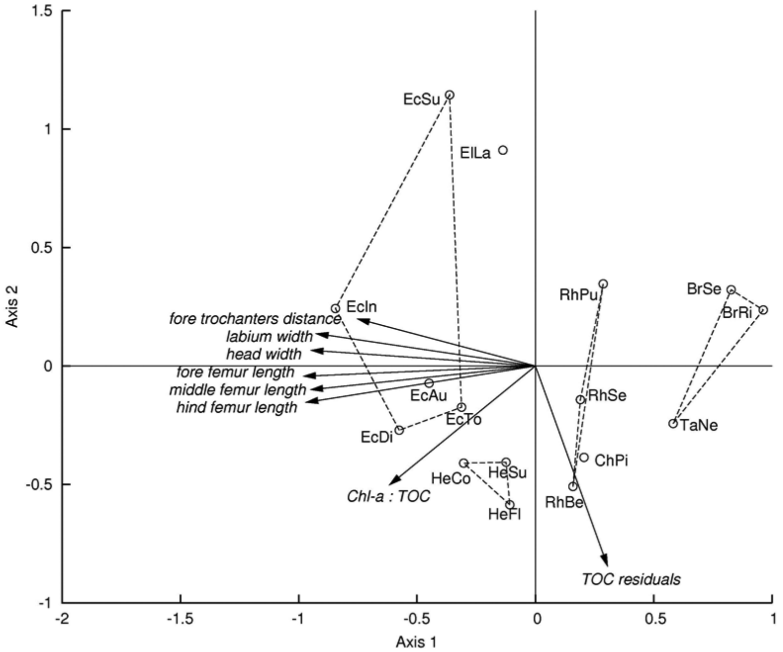

Fig. 4. Correlation biplot based on principal component analysis (PCA) of environmental characteristics and the morphological characters of aquatic insect nymphs. The morphological characters used are presented in Table II. Total organic carbon concentration (TOC) and chlorophyll-a concentration to TOC ratio (Chl-a : TOC) were used as environmental characteristics. TOC residuals from the linear regression analysis of both variables with TOC as dependent variable were used instead of TOC. The axes 1 and 2 explained 70% and 13% of the variance, respectively. Species are grouped according to their life forms and the groups are delineated with convex hulls. The species scores (points) were multiplied by 0.5. Abbreviations in Table II, except EcTo – *Ecdyonurus torrentis* and *E.* cf. *torrentis*.

Table II. Body length and the size of some body parts of selected mayfly and stonefly species nymphs in proportion to the length of the thorax and abdomen together (%). Mostly specimens with long wing-pads were measured (all except one *Heptagenia coerulans* and one *Electrogena lateralis*). ^{a}Head width was measured in front of eyes in the marked species.

Species	Abbreviation	Body length (mm)		Body length measured (mm)	Number of specimens measured	% of the length of thorax and abdomen together						
		Bauernfeind, Humpesch (2001)	Landa (1969)			Head width	Labium width	Distance of lateral margins of paraglossae	Distance of trochanters of forelegs	Fore femur length	Mid femur length	Hind femur length
Ecdyonurus aurantiacus (Burmeister, 1839)	EcAu	9-11	8-12	9.8	4	35	29	21	21	27	29	33
Ecdyonurus insignis (Eaton, 1870)	EcIn	10-13	10-13	10.5	3	39	29	21	24	31	34	36
Ecdyonurus dispar (Curtis, 1834)	EcDi	11-14	9-14	10.2	5	37	30	21	23	28	31	34
Ecdyonurus submontanus Landa, 1969	EcSu	10-14	10-12	12.9	6	36	28	20	20	28	30	33
Ecdyonurus torrentis Kimmins, 1942	EcTo	14-18	10-14	15.2	7	38	26	19	22	27	29	31
Ecdyonurus venosus (Fabricius, 1775)		10-16	10-18	14	1	35	26	18	21	26	29	
Electrogena lateralis (Curtis, 1834)	ElLa	8-10	10-14	9	2	32	27	18	19	26	28	30
Electrogena ujhelyii (Sowa, 1981)	ElUj	8-10		10.3	2	34	25	18	18	28	31	32
Epeorus assimilis Eaton, 1885	EpAs	14-20	13-18	14.6	4	28	21	11	19	25	30	31
Heptagenia flava Rostock, 1878	HeFl	12-14	12-16	15.8	7	29	23	14	16	26	30	32
Heptagenia coerulans Rostock, 1878	HeCo	10-14	11-14	11	2	31	23	15	17	28	33	34
Heptagenia sulphurea (Müller, 1776)	HeSu	10-12	10-12	11.3	6	29	25	17	16	27	29	32
Rhithrogena beskidensis Alba-Tercedor & Sowa, 1987	RhBe	6-10		7.7	5	30	25	14	16	23	23	30
Rhithrogena semicolorata (Curtis, 1834)	RhSe	9-13	9-11	9.6	8	29	23	13	16	21	24	29
Rhithrogena cf. *puytoraci* Sowa & Degrange, 1987	RhPu	9-12		10.5	7	29	22	12	14	21	24	28
Choroterpes picteti (Eaton, 1871)	ChPi	8-11	8-11	7	1	23^{a}	20	16	11	23	26	29
Potamanthus luteus (Linnaeus, 1767)	PoLu	11-15	11-14	15.1	5	12^{a}	7		8	16	14	17
Paraleptophlebia submarginata (Stephens, 1835)	PaSu	10-14	8-12	10.8	5	15^{a}	10		6	17	17	18
Habroleptoides confusa Sartori & Jacob, 1986	HaCo	9-12	8-11	8.8	5	14^{a}	8		9	13	13	16
Habrophlebia lauta Eaton, 1884	HaLa	7-9	6.5-8	5.6	4	17^{a}	11		6	18	16	20
Oligoneuriella rhenana (Imhoff, 1852)		12-16	10-17	15.8	2				21	13	17	20
Taeniopteryx nebulosa (Linnaeus, 1758)	TaNe			8.5	1	18	13		18	20	22	26
Brachyptera risi (Morton, 1896)	BrRi			10	2	15	13		14	15	17	21
Brachyptera seticornis (Klapálek, 1902)	BrSe			10	2	16	16		15	16	19	22

lated with each other. *Brachyptera braueri* had to be excluded from the analysis, because the adults of this species emerge in early spring (March--April, Soldán *et al.* 1998) and thus the high mean Chl-a : TOC value at the site cannot be used to describe its environment. *Brachyptera risi* (Morton, 1896) and *Brachyptera seticornis* (Klapálek, 1902) fly later (March-June, Soldán *et al.* 1998).

In Figs 5-9, the distribution of some species is shown in relation to TOC and Chl-a : TOC ratio, based on presence/absence data. The least-square regression lines are used to demonstrate the difference in the distribution of some species. For some species, mean TOC and Chl-a : TOC ratio values are given in Table III. The differences in the distribution of the genera of Heptageniidae (*Choroterpes* Eaton, 1881 of the Leptophlebiidae family is also included in Fig. 6) are more pronounced in the summer than in the winter (Figs 5 and 6).

4. Discussion

The results showed that the high-cost life forms (*Ecdyonurus*) with a wide head and long legs prefer high food quality (Chl-a : TOC) and low food quantity (TOC residuals), whereas low-cost life forms (*Brachyptera*, *Taeniopteryx*) with a narrow head and short legs prefer the opposite (Fig. 4). With increasing food quality and constant quantity, the length of the femora is increased, because there are more nutrients available to enhance the mobility. With decreasing food quantity and constant quality, the head is widened, because it enables the individual to collect more food.

The quantity of the deposited organic matter may be more important in summer, when it has high quality and may thus be more important as food. Further, the differences in quality between sites are probably larger in the summer, which may account for the greater differences in distribution of the genera of Heptageniidae in the summer than in the winter (Figs 5 and 6).

Food digestion can be more temperature-sensitive than food intake (Harrison, Fewell 1995; Chown, Nicolson 2004). If the rate of food acquisition was only slightly temperature dependent and if it was interrelated with some morphological traits instead, an adaptation to a temperature could be based on a change of the morphology that would ensure the ingestion and food processing rates to be matched. This is probably why there are only winter species in the grazer genera *Heptagenia*, *Epeorus* and *Brachyptera* (Soldán *et al.* 1998; Bauernfeind, Humpesch 2001) which have a relatively narrow head, while there are both winter and summer species in the genera *Ecdyonurus*, *Electrogena* and *Rhithrogena* that have a relatively wide head. In such a case, the winter genus *Heptagenia* with a narrow head could be replaced with *Ecdyonurus* with a wide head in the summer (both are genera with long legs) and winter

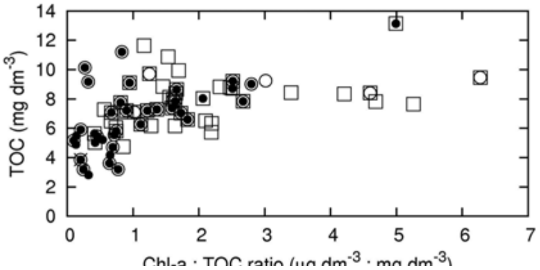

Fig. 5. Mean TOC and the chlorophyll-a to TOC ratio for the sampling sites (66 of 67 sites) where the following species were found, irrespective of their abundance: the winter species of the mayfly genera *Heptagenia* (□, *H. sulphurea*, *H. flava, H. coerulans*), *Ecdyonurus* (○, *E. torrentis*, *E. venosus*, *E.* sp.), *Rhithrogena* (●), and *Electrogena* (×, *E. lateralis*).

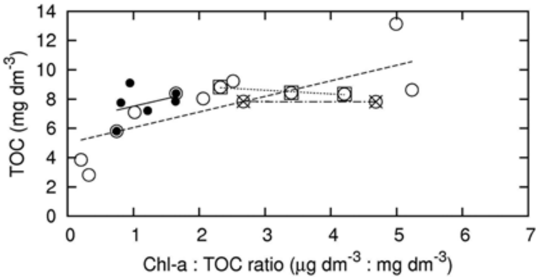

Fig. 6. Mean TOC and the chlorophyll-a to TOC ratio for the sampling sites where the following species were found, irrespective of their abundance: the summer species of the mayfly genera *Rhithrogena* (●, solid line, *R. beskidensis*), *Ecdyonurus* (○, dashed line, *E. submontanus, E. dispar*, *E. insignis*, *E. aurantiacus*), *Electrogena* (×, dashed and dotted line, *E. affinis*), and *Choroterpes* (□, dotted line, *C. picteti*). The lines are the least-square regression lines.

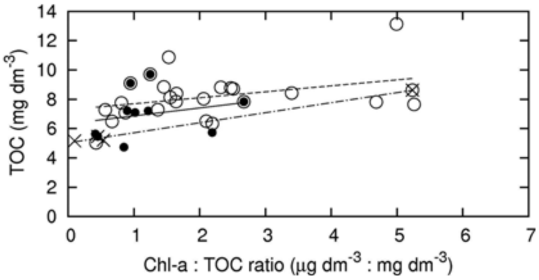

Fig. 7. Mean TOC and the chlorophyll-a to TOC ratio for the sampling sites where the following species were found, irrespective of their abundance: the caddisfly species *Brachycentrus subnubilus* (○, dashed line), the stonefly species *Taeniopteryx nebulosa* (●, solid line) and the stonefly genus *Brachyptera* (×, dashed and dotted line): *Brachyptera risi* (one point on the left), *B. seticornis* (two points in the middle), *B. braueri* (one point on the right). The lines are the least-square regression lines.

Brachyptera could be replaced with *Rhithrogena* in the summer (both are genera with short legs). Indeed, the mean values of TOC and Chl-a : TOC ratio are at the sites with the summer species of the genera *Rhithrogena*, *Ecdyonurus* and *Choroterpes* higher than at the sites with the winter species of the genera *Rhithrogena*, *Ecdyonurus* and *Heptagenia* (Table III). Here, *Choroterpes* seems to be a summer equivalent of the winter genus *Heptagenia*. The short-legged genera are probably low-cost regarding their legs and thus they prefer high food availability, especially if the food is low quality, so that there is a decreased need to escape predators (see *Rhithrogena beskidensis* Alba-Tercedor & Sowa, 1987 in Fig. 6), or if their adults emerge in early spring, so that they only live in cold environment with low food quality in the winter (*Brachyptera braueri* in Fig. 7).

The mayflies *Potamanthus luteus* of the Potamanthidae family, *Paraleptophlebia submarginata*, *Habroleptoides confusa,* and *Habrophlebia lauta* (Leptophlebiidae) are all the life form of sprawlers feeding as collectors-gatherers (Merritt, Cummins 1996; Bauernfeind, Humpesch 2001; Wichard *et al.* 2002), similar in shape, but different in size (Table II). *Potamanthus luteus* also filters food passively (Elpers, Tomka 1994). The size of the life form increases in the sequence *Habrophlebia lauta*, *Habroleptoides confusa, Paraleptophlebia submarginata*, and *Potamanthus luteus* (Table II) with increasing both food quantity and quality (Table III). The reason may be their size: larger species probably need more benthic organic matter. The greater is the amount of the particulate organic matter in water, the larger are the places with sufficient food supply. However, food quality has to increase, too, because otherwise the life form could be replaced with some low-cost one. Conversely, if food quality only increased, the life form could be replaced with a high-cost one.

Taeniopteryx nebulosa (Linnaeus, 1758) and *Brachyptera braueri*, both members of the family Taeniopterygidae of Plecoptera, were once re-

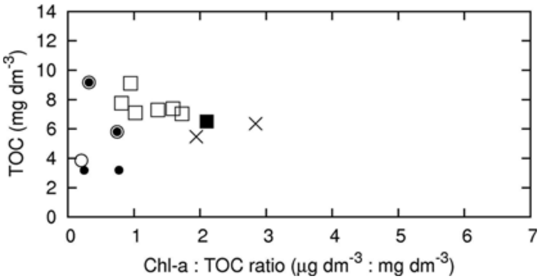

Fig. 8. Mean TOC and the chlorophyll-a to TOC ratio for the sampling sites where the following species were found, irrespective of their abundance: the stonefly species of the Perlidae family: *Dinocras cephalotes* (●), *Perla marginata* (○), *Perla burmeisteriana* (□), and *Agnetina elegantula* (■).Two sites from the Rába River (Rába in Rum and Arpás according to OKIR (2012), data from 2007-2009) with recent literature records of *Marthamea vitripennis* (Perlidae) from Hungary (Kovács, Ambrus, 2001) are also shown (×).

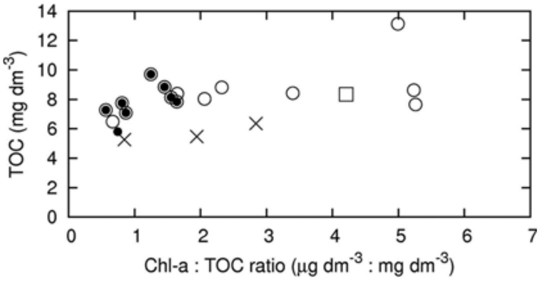

Fig. 9. Comparison of the distribution of *Perlodes* spp. (●) and *Brachycentrus subnubilus* (○), irrespective of their abundance, in relation to mean TOC and the chlorophyll-a to TOC ratio in rivers. All sampling sites with streamflow over 10 m^3 s^{-1} are shown. In one sampling site (□), none of both organisms was found. Three sites with streamflow over 10 m^3 s^{-1} from the Rába and Lapincs Rivers (Lapincs in Szentgotthárd; Rába in Rum and Arpás; according to OKIR (2012), data from 2007-2009) with recent literature records of *Marthamea vitripennis* (Perlidae) or *Isogenus nubecula* (Perlodidae) from Hungary (Kovács, Ambrus 2001) are also shown (×).

Table III. Mean TOC and Chl-a : TOC ratio values of the sites with selected species, irrespective of the abundance of the species.

	Chl-a : TOC (μg dm^{-3} : mg dm^{-3})	**TOC (mg dm^{-3})**
Epeorus assimilis	0.4	5.7
Rhithrogena spp. (winter species)	1.1	6.7
Ecdyonurus spp. (winter species)	1.4	7.2
Heptagenia spp. (winter species)	1.9	7.8
Rhithrogena spp. (summer species)	1.2	7.7
Ecdyonurus spp. (summer species)	2.6	7.7
Choroterpes picteti (summer species)	3.3	8.5
Heptagenia sulphurea	1.9	7.7
Heptagenia flava	2.2	8.3
Habrophlebia lauta	0.4	6.1
Habroleptoides confusa	1	6.8
Paraleptophlebia submarginata	1.7	7.2
Potamanthus luteus	2.4	8.3

ported from low-altitude rivers (Klapálek 1905; Illies 1955; Lillehammer 1988; Landa *et al.* 1997; Soldán *et al.* 1998). During this study, *T. nebulosa* was mostly found in brooks with low food quality, whereas *B. braueri* was only found at one site, the Berounka River (Praha-Radotín) with a high food quality (Fig. 7). In Fig. 7, the caddisfly (Trichoptera) *Brachycentrus subnubilus* Curtis, 1834 was included as a common species of lowland rivers. It is a little mobile passive filterer (Waringer, Graf 1997) with a large abdomen, which can thus be regarded as low-cost life form tolerating higher food quantity than *T. nebulosa*. The species of the genus *Brachyptera* are generally clingers in current feeding as grazers (Wichard *et al.* 2002). *T. nebulosa* is a sprawler or clinger feeding as a shredder or collector (Lillehammer 1988; Merritt, Cummins 1996), living in the pool zone of streams (Soldán *et al.* 1998). Both *Brachyptera* and *Taeniopteryx* have a narrow head. Therefore, they probably both prefer to gather food in places with high food quantity. If there is little suspended organic matter in water, such places are probably more distant from each other. Then, the ability of *Brachyptera* to move and collect food in current is advantageous and *Brachyptera* thus prefers lower quantity of suspended organic matter than *Taeniopteryx* (Fig. 7).

Both Perlidae and Perlodidae predatory stoneflies can live in lowland rivers (Klapálek 1905; Illies 1955; Graaf 1997; Landa *et al.* 1997; Soldán *et al.* 1998). The stoneflies of the family Perlidae were only found at sites with low food quality (Fig. 8), including *Perla burmeisteriana* Claassen, 1936 and *Agnetina elegantula* (Klapálek, 1907) which can inhabit lowland rivers. The same applies to *Perlodes* Banks, 1903 in the rivers with streamflow over 10 m^3 s^{-1} (Fig. 9). In Fig. 9, all sites with streamflow over 10 m^3 s^{-1} are shown. The distribution of the caddisfly *Brachycentrus subnubilus* was included in Fig. 9 to indicate that there was a current sufficient for this passively filtering species. Lowland river species *Marthamea vitripennis* (Burmeister, 1839) (Perlidae), and *Isogenus nubecula* Newman, 1833 (Perlodidae) are extinct today in the Czech Republic (Helešic *et al.* 2005). However, they have been recently found in the rivers Rába (*M. vitripennis*) or Rába and Lapincs (*I. nubecula*) in Hungary (Kovács, Ambrus 2001). The data on TOC and Chl-a : TOC ratio from these rivers from 2007-2009 according to OKIR (2012) were included in Figs 8-9. As low TOC values as in these rivers were not found in any river with streamflow over 10 m^3 s^{-1} included in the present study (Fig. 9). The streamflow of Lapincs and Rába is 13 m^3 s^{-1} and 27 m^3 s^{-1} , respectively (Magyar Nagylexikon, 1993-2004). In comparison to other species of Perlidae, *M. vitripennis* probably requires higher Chl-a : TOC ratio values accompanied by low TOC values (Fig. 8). The predatory stoneflies (Perlidae and Perlodidae) can be regarded as high-cost life forms in comparison to little mobile predators with either large abdomen like *Hydropsyche*, or without legs at all, like leeches (Hirudinea). With increasing both food quality (Chl-a : TOC ratio) and quantity (TOC), the abundance of the prey probably increases and the high-cost life form of Perlidae and Perlodidae may be replaced by low-cost life forms.

The data support the hypothesis that the benthic detritivore and herbivore macroinvertebrates that are high-cost life forms prefer high food quality and low food quantity in comparison with the low-cost life forms. The high-cost features are especially a wide head and long legs. The high-cost predators probably prefer low abundance of prey which may be caused by both low food quality and low food quantity. Total organic carbon concentration in water can be used to estimate food quantity for benthic macroinvertebrates, and chlorophyll-a to total organic carbon concentration ratio may be suitable to estimate food quality.

The quantity and quality of the organic matter in streams may be influenced by catchment properties such as altitude and vegetation, or by human activities such as waste water input. It changes in reservoirs. It may also change from year to year, possibly affecting benthic macroinvertebrate population density. The different preferences for the composition of organic matter may account for the different distribution patterns of rare and endangered species.

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