



Longitudinal zonation of larval *Hydropsyche* (Trichoptera: Hydropsychidae): abiotic environmental factors and biotic interactions behind the downstream sequence of Central European species

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Received: 27 January 2021 / Revised: 13 April 2021 / Accepted: 21 April 2021 / Published online: 13 May 2021
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Abstract The aim of this review is to summarize the literature knowledge about how abiotic environmental factors and biotic interactions affect the sequentially overlapping longitudinal distribution of Central European species of the net-spinning freshwater caddisfly larvae of the genus *Hydropsyche* (Trichoptera: Hydropsychidae). In this relation, several physical and chemical parameters of water are discussed, as well as different species-specific traits, behavioural aspects and the interaction of coexisting species. Longitudinal gradients of river networks, especially annual temperature range, flow velocity and the particle size of suspended food material play a crucial role in forming the downstream succession of characteristic species, while increased levels of organic pollution, nutrients, salinity and heavy metals

facilitates the presence of more tolerant ones. Several species-specific traits, such as respiration range, net-building frequency, head capsule size or optimal net-building velocity correlate with the position of a given species in the sequence. Coexistence of species with similar ecological demands in the overlapping zones of distribution is facilitated by differences in feeding and net-building habits, microhabitat preferences and staggering life cycles, but complicated at the same time by means of inter- and intraspecific territorial behaviour, such as fighting for the ownership of larval retreats or the practice of stridulation.

Keywords Hydropsychidae · Longitudinal distribution · Abiotic factors · Biotic interactions

Handling editor: Verónica Ferreira

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Introduction

A fundamental concept of ecology is that organisms exist in a multidimensional space, a so called *niche*, where the dimensions—interpreted as hypothetical axes of various quantifiable environmental factors—have impacts on one particular organism or population which, in return has responses and also possible impacts on these factors (Hutchinson, 1957; MacArthur & Levins, 1967; Schoener, 1989; Chase & Leibold, 2003). The number of types, forms, measures and scales of such factors is vast and their

importance is well known at all ecological (i.e. individual, population, species, community and ecosystem) levels (e.g. Hynes, 1970; Dunson & Travis, 1991; Jackson et al., 2001; Bornette & Puijalon, 2011; González-Salazar et al., 2013; Zellweger et al., 2016). Identifying these factors and modelling their effects on the distribution of species is a key issue in ecology (Araújo & Guisan, 2006; Ashcroft et al., 2011).

Environmental factors and processes acting at different scales from the level of individual biotic interactions to the effect of different temperature regimes are considered to be the key driving forces behind species' distribution either viewed from their local abundances in a counteracting metacommunity of populations or their presence-absence in a certain geographical area (Weiher & Keddy, 1999; Soberón, 2010; Boulangeat et al., 2012; Thuiller et al., 2015).

Being exceptionally rich and diverse considering their fauna and flora, yet showing distinctive similarities worldwide regarding longitudinal structure, dynamics, environmental gradients and functional species groups (Illies, 1961; Cummins, 1974; Vannote et al., 1980; Statzner, 1987; Schmidt-Kloiber et al., 2017; Englmaier et al., 2020), riverine ecosystems are thoroughly studied sites for understanding the role of environmental factors in the spatiotemporal distribution of freshwater species.

Benthic invertebrates, one of the most prominent functional group of aquatic organisms (Faith & Norris, 1989; Resh & Rosenberg, 1993; Wallace & Webster, 1996) are found in most lotic freshwater habitats, where they are key components of aquatic food webs and develop high diversity both from taxonomical and functional point of view (Hellowell, 1986). Due to their sedentary lifestyle and a wide range of sensitivities and tolerance of nearly any nature of changes in both water quality and habitat characteristics, their distribution is the result of site-specific ecological conditions at almost every spatial scale from microhabitats to whole river networks (Richards et al., 1997; Dolédec et al., 2000; Malmqvist, 2002; Li et al., 2001, 2010).

The net-spinning larvae of Hydropsychid caddisflies (Trichoptera: Hydropsychidae) have been the subject of ecological investigation since the 1970's due to (1) their essential service as filter-feeders/collectors and processors of suspended organic materials (Cummins, 1973; Wallace et al., 1977; Fuller &

Mackay, 1980; Wallace & Merritt, 1980; Hauer & Stanford, 1982); (2) the variety of their pollution and disturbance tolerance among species—therefore their use as bio-indicators (Higler & Tolkamp, 1983; Hellowell, 1986; Dohet, 2002; Houghton, 2004); (3) their importance as ecosystem engineers, since they physically modify, maintain and create their own habitat substrate (see Cardinale et al., 2004; Maguire et al., 2020); and (4) most notably the species' well-pronounced longitudinal zonation along the stream-river continuum, which is considered to be the result of combined effects of several abiotic, biotic and (bio-)geographical factors (e.g. Décamps, 1968; Badcock, 1974; Gordon & Wallace, 1975; Wiggins & Mackay, 1978; Hildrew & Edington, 1979; Ross & Wallace, 1982; Dolédec & Tachet, 1989; Roux et al., 1992).

The aim of the current review is to summarize and discuss the literature and knowledge about the environmental factors and biotic interactions influencing the longitudinal distribution of larval Hydropsychidae with special reference to Central European species of the genus *Hydropsyche* Pictet, 1834, establishing a baseline inventory for further research and application of the group as model organisms. As the identification and compilation of decisive environmental factors are basic and inevitable steps of descriptive or predictive species distribution modelling—a widespread design in aquatic ecology—we would also highlight the need of similar works for other freshwater faunal groups and other geographic areas.

Central European species of the genus *Hydropsyche* and the longitudinal sequence

In Central Europe—defined by Waringer & Graf (2011) as Austria, Germany and Switzerland with the whole extent of Ecoregion 9 (Illies, 1978), and expanded here to include Ecoregion 11 (Hungarian Lowlands) (see Fig. 1)—20 species of the genus *Hydropsyche* are known (Neu & Tobias, 2004; Graf et al., 2008; Waringer & Graf, 2011), 18 of which are treated in this review (Table 1). *Hydropsyche tobiasi* Malicky, 1977—a species known only by adult collection specimens—though listed in some sources (e.g. Neu & Tobias, 2004; Robert, 2004) as a member of the Central European caddisfly fauna, has not been caught since 1938, and widely considered to be extinct

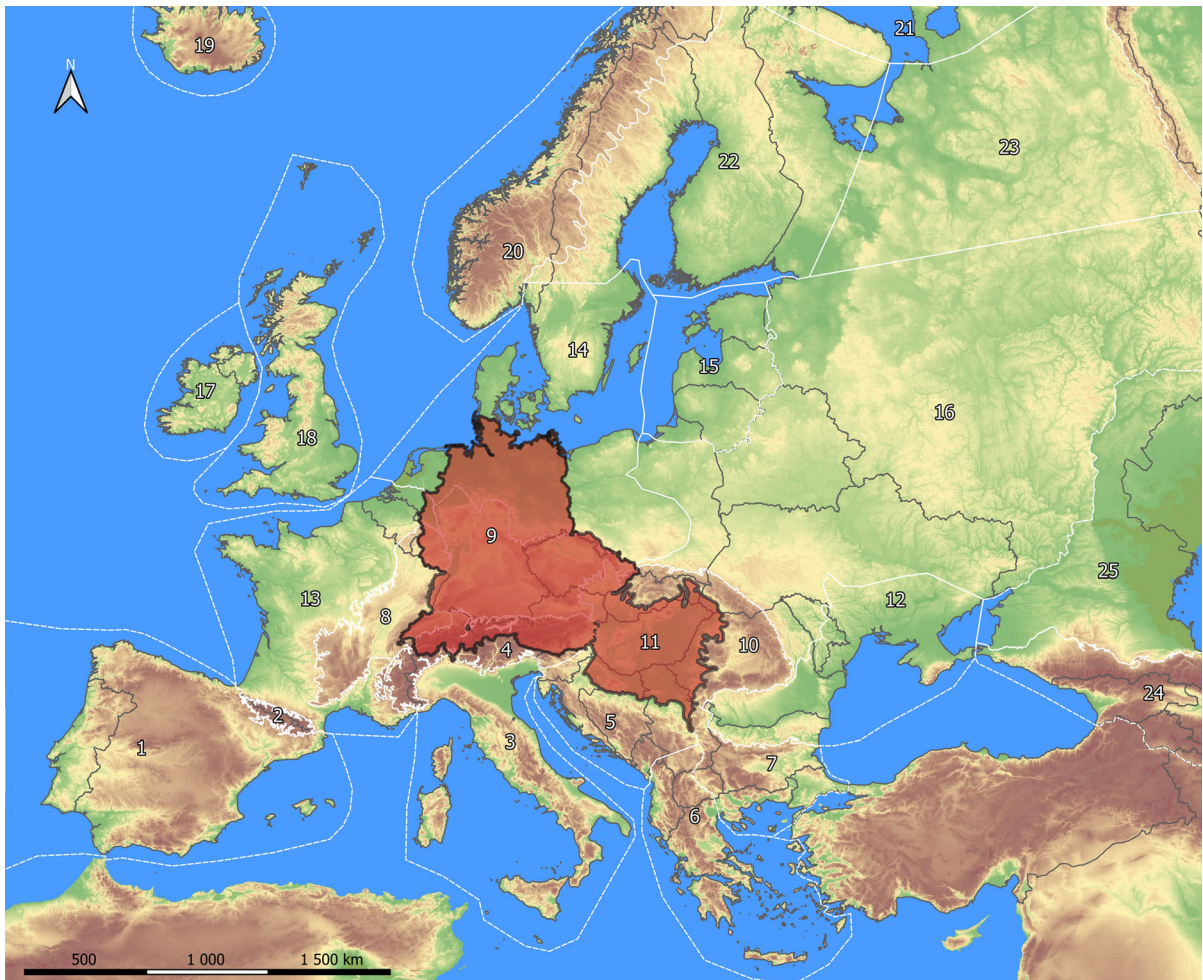


Fig. 1 Map showing the Central European area covered in this review (darkened). It includes Austria, Germany and Switzerland as well as the whole extent of European Ecoregion 9 and 11

(Malicky, 2014), thus not treated in this review. The *Hydropsyche doehleri* Tobias, 1972 has also been excluded from our review, because this species basically has Mediterranean distribution (Calabria, Sicily, Sardinia and Corsica) and its range only marginally reaches the Central European region in the canton of Ticino, Switzerland (Vincentini et al., 2020).

Based on morphological characteristics of the adults, Malicky (1977) and Pitsch (1993) define four species groups (for full species names see Table 1): (1) *H. instabilis*-Group (containing *H. instabilis*, *H. siltalai*, *H. tenuis*, *H. saxonica* and *H. fulvipes*), (2) *H. pellucidula*-Group (*H. pellucidula*, *H. incognita*, *H. dinarica* and *H. botosaneanui*), (3) *H. guttata*-Group

as proposed by Illies (1978). Numbers refer to European Ecoregions defined by Illies (1978)

(*H. guttata*, *H. bulgaromanorum*, *H. ornatula*, *H. contubernalis*, *H. tobiasi*, *H. modesta*, *H. exocellata* and *H. bulbifera*) and (4) *H. silfvenii*-Group (only *H. silfvenii* with central European distribution) with one species, *H. angustipennis*, that cannot be assigned to any of the above-mentioned groups. Different grouping of the genus can also be found in the literature (e.g. Malicky & Chantaramongkol, 2000), and more recent studies define all *Hydropsyche* species as part of the *H. instabilis*-Group based on molecular evidence (see Geraci et al., 2010). Larvae of the family generally occur in restricted parts of the stream system. Their sequential distribution extends over almost the entire river continuum from headwaters to large rivers (Fig. 2), and is so pronounced that a stream can be

Table 1 Main ecological preferences of larvae of 18 Central European *Hydropsyche* species

Species	Abbr.	Curr. pref.	Temp. pref.	Dil. O ₂ pref.	Poll. tol.	Flight per.	Stream zonation preference ¹⁶							
							eC	hC	eR	mR	hR	eP	mP	hP
<i>H. angustipennis</i> (Curtis, 1834) ¹	<i>angu</i>	▼	▲	▼	v.high	IV–IX	–	–	–	3	3	3	1	–
<i>H. botosaneanui</i> Marinkovic, 1966 ²	<i>boto</i>	n/a	n/a	n/a	n/a	V–VI	–	–	2	4	3	1	–	–
<i>H. bulbifera</i> McLachlan, 1878 ^{1,3}	<i>bulb</i>	►	n/a	n/a	high	V–IX	–	–	–	1	4	5	–	–
<i>H. bulgaromanorum</i> Malicky, 1977 ^{1,4}	<i>bulg</i>	▼	▲	▼	mod	III–X	–	–	–	1	3	3	3	–
<i>H. contubernalis</i> McLachlan, 1865 ^{1,4}	<i>cont</i>	►	▲	▼	high	IV–X	–	–	–	1	4	4	1	–
<i>H. dinarica</i> Marinkovic, 1979 ^{1,5,6}	<i>dina</i>	n/a	▼	▲	low	V–IX	–	–	4	5	1	–	–	–
<i>H. exocellata</i> Dufour, 1841 ⁷	<i>exoc</i>	►	n/a	n/a	high	IV–X	–	–	–	–	2	5	2	1
<i>H. fulvipes</i> (Curtis, 1834) ^{1,3}	<i>fulv</i>	▲	▼	▲	v.low	V–VIII	1	7	2	–	–	–	–	–
<i>H. guttata</i> Pictet, 1834 ^{1,3}	<i>gutt</i>	►	►	n/a	n/a	IV–XI	–	–	–	–	5	4	1	–
<i>H. incognita</i> Pitsch, 1993 ^{1,9}	<i>inco</i>	▲	n/a	▲	low	V–IX	–	–	–	5	4	1	–	–
<i>H. instabilis</i> (Curtis, 1834) ^{1,3,10}	<i>inst</i>	▲	▼	►	low	VII–IX	–	–	4	4	2	–	–	–
<i>H. modesta</i> Navas, 1925 ^{1,3,6}	<i>mode</i>	►	▲	n/a	high	V–IX	–	–	–	2	2	2	2	2
<i>H. ornata</i> McLachlan, 1878 ^{3,11}	<i>orna</i>	n/a	n/a	n/a	n/a	V–VIII	–	–	–	–	3	4	3	–
<i>H. pellucidula</i> (Curtis, 1834) ^{1,3,12}	<i>pell</i>	▲	►	▲	mod	V–X	–	–	1	2	4	3	–	–
<i>H. saxonica</i> McLachlan, 1884 ^{1,13}	<i>saxo</i>	▲	▼	▲	v.low	V–VI	–	2	6	2	–	–	–	–
<i>H. silfvenii</i> Ulmer, 1906 ^{3,14}	<i>silf</i>	▲	▼	n/a	n/a	V–X	–	–	–	4	6	–	–	–
<i>H. sitalai</i> Döhler, 1963 ^{1,3}	<i>silt</i>	▲	n/a	n/a	mod	VI–IX	–	–	1	5	4	–	–	–
<i>H. tenuis</i> Navas, 1932 ^{1,15}	<i>tenu</i>	▲	▼	▲	v.low	V–VI	–	–	8	2	–	–	–	–

Species	Alt. pref. ¹⁶			Hydr. pref. ¹⁶			pH ¹⁶	Feeding type ¹⁶			
	<i>g8h</i>	<i>28h</i>	<i>l2h</i>	<i>eup</i>	<i>prp</i>	<i>pap</i>		<i>ga</i>	<i>gr</i>	<i>pff</i>	<i>pr</i>
<i>H. angustipennis</i> (Curtis, 1834) ¹	0	1	1	8	2	–	ac	–	2	5	3
<i>H. botosaneanui</i> Marinkovic, 1966 ²	1	1	0	–	–	–	n/a	–	2	5	3
<i>H. bulbifera</i> McLachlan, 1878 ^{1,3}	1	1	1	8	2	–	n/a	–	2	5	3
<i>H. bulgaromanorum</i> Malicky, 1977 ^{1,4}	0	1	1	7	2	1	n/a	–	2	5	3
<i>H. contubernalis</i> McLachlan, 1865 ^{1,4}	0	1	1	8	2	–	n/a	1	–	8	1
<i>H. dinarica</i> Marinkovic, 1979 ^{1,5,6}	1	1	1	–	–	–	n/a	–	2	5	3
<i>H. exocellata</i> Dufour, 1841 ⁷	0	1	1	10	–	–	n/a	–	2	5	3
<i>H. fulvipes</i> (Curtis, 1834) ^{1,3}	1	1	1	10	–	–	ne-al	–	2	5	3
<i>H. guttata</i> Pictet, 1834 ^{1,3}	–	–	–	10	–	–	n/a	–	2	5	3
<i>H. incognita</i> Pitsch, 1993 ^{1,9}	1	1	1	10	–	–	n/a	–	2	5	3
<i>H. instabilis</i> (Curtis, 1834) ^{1,3,10}	1	1	1	10	–	–	ne-al	–	2	5	3
<i>H. modesta</i> Navas, 1925 ^{1,3,6}	0	1	1	8	2	–	n/a	–	2	5	3
<i>H. ornata</i> McLachlan, 1878 ^{3,11}	0	1	1	10	–	–	n/a	–	2	5	3
<i>H. pellucidula</i> (Curtis, 1834) ^{1,3,12}	1	1	1	10	–	–	ac	–	2	5	3
<i>H. saxonica</i> McLachlan, 1884 ^{1,13}	0	1	1	10	–	–	n/a	–	2	5	3

Table 1 continued

Species	Alt. pref. ¹⁶			Hydr. pref. ¹⁶			pH ¹⁶	Feeding type ¹⁶			
	<i>g8h</i>	<i>28h</i>	<i>l2h</i>	<i>eup</i>	<i>prp</i>	<i>pap</i>		<i>ga</i>	<i>gr</i>	<i>pff</i>	<i>pr</i>
<i>H. silfvenii</i> Ulmer, 1906 ^{3,14}	0	1	0	10	–	–	<i>n/a</i>	–	2	5	3
<i>H. siltalai</i> Döhler, 1963 ^{1,3}	0	1	1	10	–	–	<i>ind</i>	–	2	5	3
<i>H. tenuis</i> Navas, 1932 ^{1,15}	–	–	–	–	–	–	<i>n/a</i>	–	2	5	3

References for the species and preference values are indicated in upper indices

Curr. pref.—current preference, Temp. pref.—temperature preference, Dil. O₂ pref.—preference for diluted oxygen content (▲—high, ►—moderate, ▼—low), Poll. tol.—tolerance of (organic) pollution, Flight per.—flight period (number of months in latin numerals). Stream zonation preference (in ten-point assignment system): eC—eucrenal, hC—hypocrenal, eR—epirhithral, mR—metarhithral, hR—hyporhithral, eP—epipotamal, mP—metapotamal, hP—hypopotamal). Altitude preference in presence/absence assignment system: g8h—above 800 m AMSL (above mean sea level), 28h—between 200 and 800 m AMSL, l2h—below 200 m AMSL. Hydrologic preference: eup—eupotamon, prp—parapotamon, pap—palaeopotamon, pH preference: ac—acidic, ne-al—neutral to alkaline, ind—indifferent). Feeding type in ten-point assignment system: ga—gatherer/collector, gr—grazer, pff—passive filter feeder, pr—predator. *n/a*: data insufficient or not available

1: Lechthaler & Stockinger (2005); 2: Neu & Fischer (2002); 3: Waringer & Graf (1997); 4: Czachorowski & Serafin (2004); 5: De Soto et al. (1994); 6: Roux et al. (1992), 7: Guinand et al. (1994); 8: Usseglio-Polatera & Bournaud (1989); 9: Pírú et al. (2015); 10: Philipson (1954); 11: Malicky (1977); 12: Becker (1987); 13: Hrovat & Urbanič (2012); 14: Coppa (2015); 15: Pitsch (1993), 16: Graf et al. (2008)

divided to specific sections characterized by different species and their combinations (Higler & Tolkamp, 1983; Statzner & Dolédec, 2011). Larval *Hydropsychidae* typically colonize hard bottom substrates of different types and particle sizes, where they build retreats consisting of silk and substrate material with specific mesh sized catch-nets attached, facilitating their filter feeding through five larval instars. Adults of early-swarmer species (e.g. *H. angustipennis*, *H. bulgaromanorum* or *H. contubernalis*) fly from March or April while most are on wing from May to September (Waringer & Graf, 1997).

The stream section-specific *Hydropsyche* larval assemblages correspond well with the taxonomical species groups suggested by Malicky (1977) and Pitsch (1993), so hereinafter these species-group names are used for the assemblages too. Most species of the *H. instabilis*-Group inhabit headwaters and mountainous or colline small or medium sized streams (crenal and rhithral zones) while those of the *H. pellucidula*-Group are usually found in streams and rivers of the middle sections (rhithral zones) of river networks. Species of the *H. guttata*-Group live in medium sized watercourses of the lower sections of the rhithral zone and particularly in larger rivers of the potamal zones (Table 1). Larvae of *H. angustipennis*

colonize mainly rivers and streams of variable size in lower regions (Botosaneanu & Malicky, 1978; Edington & Hildrew, 1995) but can also be found in headwaters (Pitsch, 1993). *H. silfvenii* lives in smaller streams of the rhithral zone with lower mean water temperature, higher current velocities and gravel rich bottom (Lechthaler & Stockinger, 2005; Coppa, 2015).

The longitudinal sequence of larval *Hydropsyche*, although being affected by the species' areas of distribution, shows high similarities in many European watercourses and catchment areas. For example, in the case of unpolluted British running waters the sequence is typically *inst-silt-pell-cont* (Edington & Hildrew, 1995), in the Loire it was found to be *dina/inst-silt-inco-(angu)-exoc-orna-cont-bulg*, while in the Rhône catchment to be *dina-inst-silt-(angu)-inco-cont-orna-exoc* (cited by Statzner & Dolédec, 2011). Higler & Tolkamp (1983) described the sequence of Dutch species as *fulv-saxo-silt-inst-pell-(angu)-exoc-orna-cont*, although *H. exocellata* and *H. ornatula* are reported to be disappeared and *H. bulgaromanorum* to be appeared in larger rivers of the Netherlands (Higler et al., 2008). Based on the comprehensive work of Graf et al. (2008) on the distribution and quantified ecological preferences of Trichoptera, a summarized

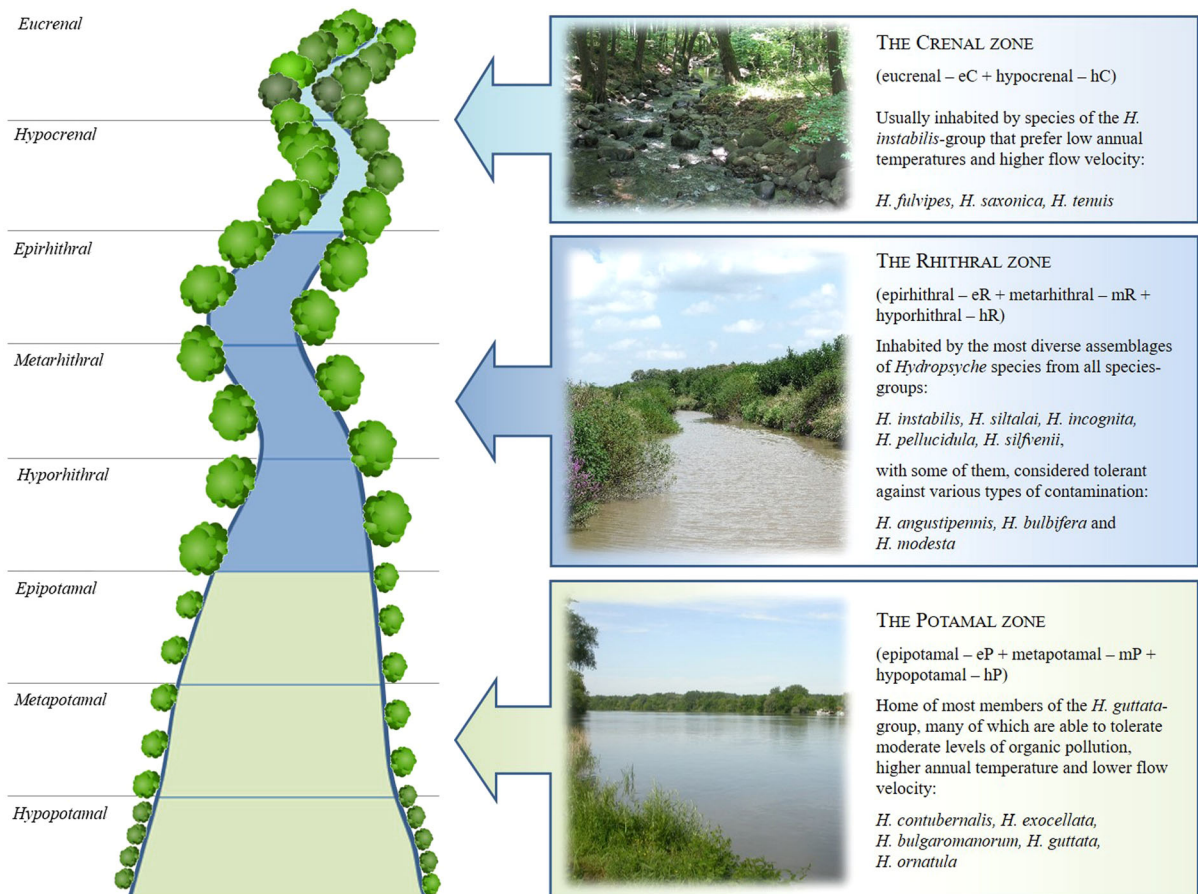


Fig. 2 Schematic and generalized view of the river continuum with the major and minor zones. Larvae of certain *Hydropsycha* species or species groups are characteristics for different parts of

downstream sequence of 18 Central European species as *fulv-saxo-tenu-dina-inst-silt-boto-pell-inco-silf-(angu)-(bulb)-(mode)-cont-bulg-gutt-orna-exoc* can be given (see Fig. 3). This sequence, however, is merely hypothetical, strongly affected by numerous environmental conditions, biased by coexistence, highly overlapping and never as complete in nature as listed here due to different geographical distribution of species. It is also notable that some species, that are less sensitive to moderate pollution levels (e.g. *H. angustipennis*, *H. bulbifera* or *H. modesta*—indicated in brackets above) do not really belong to the downstream sequence, but tend to inhabit stretches, where conditions are not suitable for less tolerant members of the genus (Higler & Tolkamp, 1983; Camargo, 1991; Statzner & Dolédec, 2011). Despite being quite common and similar in several central and

the stream system. Their sequential distribution extends over almost the entire river continuum from headwaters to large rivers

western parts of the continent, deviations from the sequence shown in Fig. 3, have been reported from some Iberian rivers, most notably the occurrence of *H. exocellata* in headwaters (Bonada et al., 2004) and the coexistence of it with *H. siltalai* and *H. instabilis* in middle and lower reaches (see Puig et al., 1987; Valladolid et al., 2007) This is possibly due to the different characteristics of the Ibero-Macaronesian ecoregion, but still calling for further inspection, since other Iberian studies (e.g. Gallardo-Mayenco et al., 1998) have shown sequences comparable to those of Central European river networks.

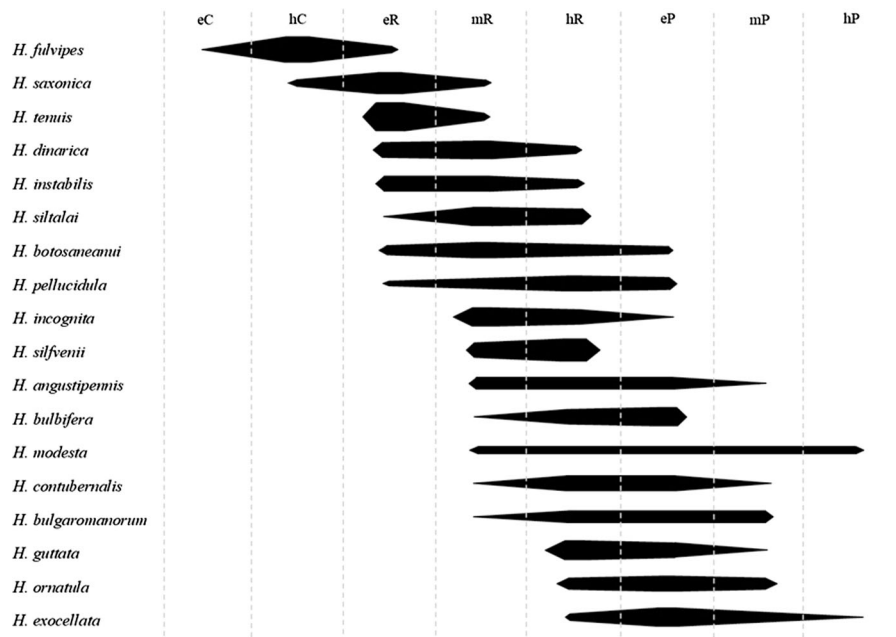


Fig. 3 Longitudinal distributional sequence of *Hydropsyche* species according to their stream zonation preference based on the data of Graf et al. (2008). Species are ordered by their first appearance and highest preference values along the river continuum. The width of plot lines corresponds with values of

preference for the indicated zones. *eC* eucrenal zone, *hC* hypocrenal zone, *eR* epirhithral zone, *mR* metarhithral zone, *hR* hyporhithral zone, *eP* epipotamal zone, *mP* metapotamal zone, *hP* hypopotamal zone

Abiotic factors influencing the distribution of larval *Hydropsyche*

Longitudinal gradient related and natural physical characteristics

Annual temperature range typically increases along the stream–river continuum towards the estuaries, but the longitudinal sequence of the species most probably is not directly related to temperature, and rather could be linked to the temperature-dependent larval metabolism (Statzner & Dolédec, 2011; Cogo et al., 2020). Although it is unlikely that the sequence of the species is the result of lethal limits in water temperature, the relationship between temperature ranges and respiratory or metabolic rates are well defined and different among species (Edington & Hildrew, 1973; Howell & Voshell, 1982; Bales & Badcock, 1987). Hildrew & Edington (1979) showed that acceleration of the respiration rate occurs at progressively higher temperatures in the downstream sequence of hydropsychid species *Dipletrona felix*, *Hydropsyche instabilis* and *H. pellucidula* in river Usk (South Wales), which is a clear sign of accommodation of downstream

species to higher temperature regimes. It also comes with an upwards extension of the range where these species show relative temperature independence, thus having extended thermal tolerance. A similar downstream succession of *H. dinarica*, *H. siltalai*, *H. pellucidula*, *H. contubernalis* and *H. modesta* was observed in the Rhône river and its tributaries by the comparison of total amplitude of metabolism values, which represent the range of mean oxygen consumption of the respective species between 5 and 25°C and which can be treated as a species-trait correlated with longitudinal zonation (Roux et al., 1992), so much so that the position of a given species in the sequence can be defined based on it (Guinand et al., 1994).

The effect of flow velocity on the distribution of *Hydropsyche* has been investigated in several studies in different ecoregions. It is established that specialization for living at different flow velocities is reflected in the species' respiratory physiology and in the form and success of their net-spinning activities (Hildrew & Edington, 1979). For European species Tachet et al. (1992) remarks that the downstream trend in species succession depends on the species' ability to spin a catch net when the current velocity decreases. In

general, net-spinning activity of species living in the crenal or upper-rhithral zones increases with increasing velocity (e.g. in the case of *H. instabilis*, *H. siltalai* or *H. angustipennis*) but decreases after reaching a maximum, showing rather ubiquitous flow preference in case of species of middle reaches and the potamon, like *H. pellucidula*, *H. contubernalis* or *H. modesta* (Philipson, 1954; Edington, 1965; 1968; Becker, 1987; Tachet et al., 1992). Although the differences are slight, they on the one hand allow downstream species with broader velocity spectra to colonize slower patches of middle river sections where riffles and pools occur together (Boon, 1978), and on the other hand they provide the possibility for coexisting species to partition common habitats within the same river section (Hildrew & Edington, 1979).

The amount of dissolved oxygen also has an impact on the distribution of net-spinning caddisflies primarily by the means of net-spinning activity and behavioural changes, although its effects are highly correlated with current velocity. Long-term experiments concerning the net-building activity and larval development of *Hydropsyche* species showed that euryoecious species, such as *H. contubernalis*, are able to build capture nets with regular meshes at an O₂-saturation of only 30% and half of the examined larvae developed into adults at 50%. The less tolerant *H. pellucidula* reacts more severely to a reduction in O₂-concentration, so that development into an imago is no longer possible below a saturation of 85% (Becker, 1987). Under experimental conditions in still water with decreasing oxygen concentration the swift-water species, *H. instabilis* become immobilized at relatively higher values compared to those found for slow-water species. This difference, however, disappears provided the water is flowing or stirred, and larvae can also compensate for low oxygen concentration by current-producing abdominal movements (Philipson, 1954, 1969; Philipson & Moorhouse, 1974). Rarely being a lethal or exclusively limiting factor in their natural habitats, dissolved oxygen still considered important in the sequential distribution of the genus, as showed in the case of *H. incognita* (Pírvo et al., 2015), *H. dinarica* and *H. siltalai* (Roux et al., 1992) and also *H. angustipennis* (Vuori, 1995; van der Geest, 2007) in addition to the above mentioned.

The downstream reduction of riverbed particle size has been recognized long ago (e.g. Sternberg, 1875) and several authors established a relation between the

longitudinal distribution of different hydropsychid species and the structure of their nets, defining that species of small rivers spin nets with larger meshes than those of large rivers (Wallace, 1975; Wallace et al., 1977; Alstad, 1980, 1982; Fuller & Mackay, 1980; Fuller et al., 1983). The suggestion that net structures, especially the size of their meshes are directly related to sediment particle size comes easy, yet later studies showed that the differences of the net, though being obvious among, but less within species groups, can not be related to the longitudinal distribution of larvae (Tachet et al., 1987) and that it is most likely the result of the differences in the size of the suspended food material available (Alstad, 1982).

In a study on the distribution of *H. incognita* Pírvo et al. (2015) defined pH as the most important physico-chemical variable influencing the species distribution. However, no similar evidences are available for other European net-spinning caddisfly species, which suggests that changes of pH in natural environments affects Hydropsychidae only in extreme cases, i.e. when localized acidic pollution is obvious. Hesthagen et al. (2011) contributes the reappearance of *H. siltalai* in the tributaries of Lake Saudlandsvatn to the improvement of water quality, especially pH. According to Vuori (1995), runoff from acid sulfate soils can cause morphological abnormalities and restrict the distribution of more sensitive species, such as *H. siltalai*, while has less impact on the more tolerant *H. angustipennis*. Regerand et al. (2002) revealed the toxic effect of low pH on the lipid metabolism of *H. contubernalis*, but also point out that even small changes in pH initiate biochemical adaptation mechanisms thus broaden the tolerance of species, and only serious conditions, such as a decrease below pH 4.0 can suppress their efficiency.

Inorganic factors related to anthropogenic impact

Many studies on the distribution of aquatic macroinvertebrates, including that of net-spinning caddisflies found that increased levels of organic and inorganic forms of phosphorous and nitrogen influence the distribution of these organisms, although the effect is considered indirect (Urbanič & Toman, 2007). The findings of Vuori (1995), Buczyńska (2013) and Pírvo et al. (2015) showed that the increased presence of inorganic N- and P-forms can be related—sometimes in a major extent—to the *Hydropsyche* fauna of

streams, interpreted by the means of eutrophication processes, such as the consequential enrichment of organic matter or the decrease of dissolved oxygen due to elevated biological and chemical oxygen demand. Toxicity tests showed active migration and higher tolerance of *H. exocellata* against increased levels of NO₃-N, defining median lethal concentration (48 h LC50) at 592,3 mg/l, such conditions, however, occur very rarely under natural conditions and only in case of severe point-source nutrient pollution (Camargo et al., 2005).

Salinity can also have an effect on benthic communities as well as on the distribution of Hydropsychidae depending on the salt sensitivity of species (Zinchenko & Golovatyuk, 2013). Piscart et al. (2005) found that the abundance of *H. contubernalis* and *H. pellucidula* decreased significantly in relation to the salinity level while *H. exocellata* became more abundant at the same time. Findings of Gallardo-Mayenco et al. (1998) and Gallardo-Mayenco & Ruíz (2007) also prove *H. exocellata* to be a salinity tolerant species, but imply at the same time that salinity has an effect on the composition of the assemblages rather than on the distribution of individual species. An example of this is the case of the hydropsychidae fauna of rivers Werra and Weser in Germany, which significantly improved by the decrease of anthropogenic salt-load (Bäthe & Coring, 2011). The effect of salt pollution, conductivity and different levels of ionic components on Hydropsychidae were also tested by several authors (see Sala et al., 2016), classifying *H. instabilis* as halophobic and *H. exocellata* as halotolerant species.

Heavy metals have complex and hardly acute but rather chronic effects on *Hydropsyche* species, resulting in growth and/or developmental disorders, or affecting their fecundity, fitness or life cycles (Tszedel et al., 2016). They can be responsible for fluctuating asymmetry in *H. exocellata* (Bonada et al., 2005), changes of larval anal papillae in *H. pellucidula* (Vuori & Kukkonen, 1996) or faulty construction of filter nets (Tessier et al., 2000), as well as behavioural anomalies in *H. siltalai* and *H. contubernalis* (Vuori, 1994) or *H. angustipennis* (van der Geest et al., 1999). Generally, Hydropsychidae are among the less sensitive taxa of macroinvertebrates considering heavy metal pollution, placed in the middle of a hypothetical scale of tolerance (Barata et al., 2005), with *H. angustipennis* regarded as the most tolerant of them all

(Vuori, 1995). The harmful effects of heavy metals depend on synergistic interactions of many environmental factors, such as water temperature, current velocity and pH (Solà et al., 2004).

Organic pollution

Organic pollution of freshwater ecosystems, in its most general term means the elevated concentrations of organic compounds (usually suspended proteins, carbohydrates, fats and nucleic acids) and microorganisms living on solid particles of them as a substrate. The most typical sources of organic pollution reaching riverine systems are wastewater sewage, agricultural activities and livestock farming (Friberg et al., 2010). Expressed either as the single parameter of biological oxygen demand (BOD) (e.g. European Commission, 2000) or as a part of multimetric indices taking inorganic forms of phosphorous and nitrogen also into account (e.g. IPO—Leclercq & Maquet, 1987), the level of organic pollution has a complex and inevitable effect on macroinvertebrates and so on net-spinning caddisflies, which are among the most suitable bio-indicator organisms to reflect it (Higler & Tokamp, 1983; Hellawell, 1986).

Many studies and authors have categorized Central European *Hydropsyche* species based on their tolerance against organic pollution, and—as its level usually shows a longitudinal downstream gradient in European river systems (Mishall et al., 1985; Wen et al., 2017)—came to the same conclusions in most cases as follows (Pitsch, 1993; Waringer & Graf, 1997; Dohet, 2002; Lechthaler & Stockinger, 2005): (1) species of headwaters, rivulets and small streams of mountainous and hilly regions are the most sensitive to organic pollution, thus restricted to the shortest stretches: *H. fulvipes*, *H. saxonica*, *H. tenuis* and *H. dinarica*; (2) a bit more tolerant (but still showing considerable sensitivity) are *H. incognita*, *H. instabilis* and *H. silfvenii*, reaching even the hyporhithral zone in some territories; (3) species mainly living in the middle (rhithral) reaches are more tolerant thus having a broadened and potentially more overlapping place in the downstream sequence (*H. pellucidula* and *H. siltalai*); (4) *H. bulbifera*, *H. bulgaromanorum*, *H. contubernalis*, *H. exocellata* and *H. modesta* (the latter four inhabiting mainly the lower rhithron and potamon) are considered to be the most tolerant; and (5) *H. angustipennis*, placed at the end of the gradient, being

able to survive in various types of heavily contaminated waters at different altitudes.

The large range of sensitiveness to organic pollution, provided that other restrictive conditions, such as temperature regime, flow characteristics and microhabitat types are eligible, allows tolerant species to some extent to infiltrate or completely take over sites that become unsuitable for the more sensitive ones that otherwise could be expected (Higler & Tolkamp, 1983; Vuori, 1995; Stuijzand et al., 1999) and also allows them to return first to previously abandoned stretches in case of improving water quality (Engels et al., 1996).

Biological characteristics of *Hydropsyche* species affecting the distribution

Some species-specific traits, especially respiration range (metabolic rate), current preference, the characteristics of the net and net-building behaviour or the size of the head capsule correspond to the primary position of a given species in the longitudinal sequence of distribution (Fig. 4), and also its

possibilities to coexist with others in the same reach. Moreover, these traits show strong relation to the phylogeny of the genus: the downstream increase of respiration range, decrease of the optimal net-building velocity and frequency of net-building with regular meshes at an elevated near-bottom velocity, the decrease of net mesh size and the decrease of larval size reflects the downstream evolutionary pathway in running waters (Fig. 4) (Statzner et al., 2010; Statzner & Dolédec, 2011).

Although it is clear, that headwater species are rare downstream and large river species always absent from headwaters, generally two or exceptionally three species may occur together in the upper and middle sections of river networks, while several—even up to seven—species can coexist in the lower ones (Bournaud et al., 1982).

Several investigations were carried out to reveal the causes and strategies that allow Trichoptera species with similar ecological demands to occur together (e.g. Edington, 1968; Elliot, 1968; Wallace, 1975; Oswood, 1976; Williams & Hynes, 1973; Wallace et al., 1977; Hildrew, 1978), and many of them stress the importance of microhabitat selection in the

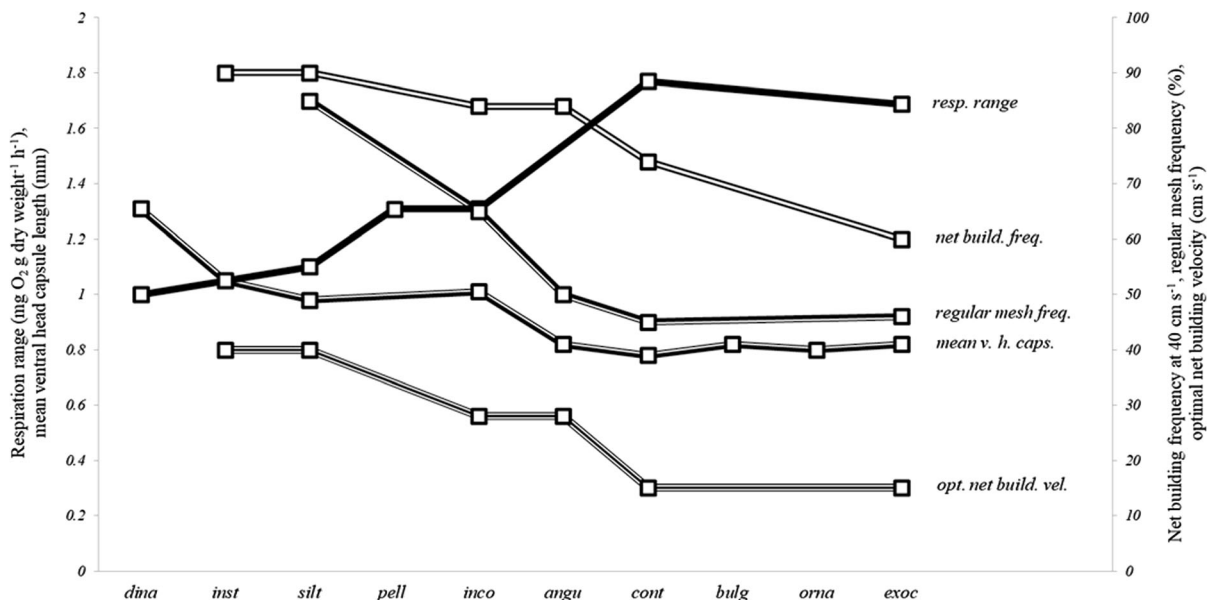


Fig. 4 Traits of some *Hydropsyche* species correlating with their position in the longitudinal sequence. Respiration range across 5–25°C (referred also as total amplitude of metabolism in the text) increases while net-building frequency and the ratio of regular meshes built at 40 cm/s, the optimal net-building velocity at which most larvae build nets with regular meshes

as well as the mean ventral length of the head capsule decreases downstream. Values of respiration range and mean ventral head capsule length are on the primary (left), others are on the secondary (right) vertical axis of the graph. (Data from Guinand et al. (1994) and Statzner & Dolédec (2011), neighbouring points are connected in case of missing values.)

coexistence in different ecoregions (e.g. Cudney & Wallace, 1980; Edington et al., 1984; Urbanic & Toman, 2005). Hildrew & Edington (1979) points out that *H. siltalai* and *H. pellucidula* divide up net-spinning sites within the same river section by partial differences in water velocity preferences, by the use of crevices of different sizes at different times (small crevices in early summer by the former and those in autumn and winter by the latter) and by the use of qualitatively different sites (e.g. those in moss or under stones). Spatial variability of net-spinning sites can also allow the coexistence with other members of Hydropsychidae, like in the case of *H. exocellata*, which is more tolerant of low current velocity, therefore was able to remain at less swift sites near the banks than in riffles, which were inhabited by *Cheumatopsyche lepida* (Pictet, 1834) (Dolédec & Tachet, 1989). According to Czachorowski & Serafin (2004), the occasionally coexisting large river species, *H. contubernalis* and *H. bulgaromanorum*, differ in their preferred habitat types as the larvae of the former were rather associated with aquatic plants, submerged parts of trees, or stones whereas those of the latter were strictly associated with large stones.

An obvious point to consider in the context of both sequential distribution and coexistence is the possible differences in net-structure and consequent specialization in diet of *Hydropsyche* species. Significant differences in net dimensions can be observed (1) between headwater and small stream species, which spin larger nets with thicker strands and coarse meshes, and those of larger rivers, which have smaller and finer structures with smaller mesh size; (2) in successive instars of larvae, where there is an increase both in overall measures and in mesh size (Kaiser, 1965; Williams & Hynes, 1973; Malas & Wallace, 1977); (3) among different genera in the family Hydropsychidae, which clearly facilitates their coexistence by partitioning food supply on the basis of particle size (Wallace, 1975; Alstad, 1982; Malas & Wallace, 1977; Wallace et al., 1977). The same instars of syntopic *Hydropsyche* species (usually belonging to the same species-group), however, have similar nets and differences in their structure only appears when different instars occur together at the same time due to their staggering life cycles, as in the case of *H. pellucidula* and *H. siltalai* in the river Usk (Hildrew & Edington, 1979).

Life histories of the *Hydropsyche* species show adaptability to environmental conditions and exhibit variations for one species, being influenced mainly by temperature both as a function of altitude and latitude (Dolédec & Tachet, 1989). Various growth rates, flight periods and overwintering larval stages of a given species were observed not only in different geographical regions but even in the same river system, for example in the cases of *H. instabilis*, *H. pellucidula*, *H. siltalai* or *H. contubernalis* (Hildrew, 1978; Andersen & Klubnes, 1983; Sieglstetter et al., 1997). These differences, including the optional change in voltinism (Tachet & Bournaud, 1981) act as isolation mechanism for coexisting species—limited by short supply of food—via different net structures as mentioned above or different feeding habits of instars, so that species, occurring at the same site, might partition resources.

The larvae of *Hydropsyche* are generally omnivorous, but they can change their behaviour and choose between hunting, grazing and catching drifting food with their nets depending on the season and on the given larval instar (Burton & McRae, 1972; Fuller & Mackay, 1980). Net-spinning activity varies by the function of complex effect of different factors, mainly temperature and current velocity, and there are certain periods during the year, especially in winter, when larvae do not spin nets at all (Xiang et al., 1984; Poepperl, 2000). By opting to choose between different strategies in their feeding behaviour, coexisting species may reduce interspecific competition (Sieglstetter et al., 1997), which, in case it appears, often results in character displacement or the retardation of the development of larvae. Both phenomena were observed in the favour of *H. pellucidula* when coexisting with *H. siltalai* (Andersen & Klubnes, 1983; Czachorowski, 1989). Gut content analyses showed that although the qualitative composition of food may change during larval instars, it is basically the same when similar instars of different species are compared (Hildrew & Edington, 1979). Differences observed in mesh size in the nets of larvae at different stages of growth appear to be related more to the selection of different kinds of food than to the selection of particles of any given size (Georgian & Wallace, 1981; Merritt & Wallace, 1981).

hydropsychidae are known to be quite territorial species; they are not only aggressive against other filter-feeders and congeneric species but also exhibit

intraspecific aggressive behaviour (Schuhmacher, 1970). The head size of the final instar affects the superiority of a given species over others, by the means of both its success to invade larval retreats of other species and defending its own retreat against invaders, and this superiority increases significantly with head length (Pierrot, 1984). Experimental evidences showed that larvae of *H. angustipennis*, *H. siltalai* and *H. pellucidula* fight vigorously about the ownership of a retreat either as intruders or defenders and also proved that victory of any party positively depends on the size of the combatant (Jansson & Vuoristo, 1979; Gatley, 1988). Losers of such fights typically escape by drift (Schuhmacher, 1970), so it has an indirect effect on larval dispersal via niche shifts or species exclusions, and which should be related to size (Statzner & Dolédec, 2011). It is also observed, that several species of *Hydropsyche* stridulate by running their fore femurs across ridges on the underside of their head when encountered with intruders of their retreat, especially in case of conspecific intruders, and that stridulation, which can also be provoked easily by nonspecific artificial stimuli, thus classed as protest sounds, increases defensive success (Jansson & Vuoristo, 1979). Fighting and stridulation, however, do not seem to have function in spacing or regulating population density as in natural conditions larvae often build their retreats side by side, sometimes even with common walls, and in such cases fighting only occurs when the larvae start building their retreats but ceases soon after. Stridulation by specimens in their own retreats is only responded by others when the shelters have common walls, and it can continue in an alternating way for hours, however, no fighting were observed in these cases, and the specimens remained in their closely situated retreats for weeks (Jansson & Vuoristo, 1979).

Conclusions

Longitudinal distribution of *Hydropsyche* species along the stream-river continuum shows a distinctive zonation or overlapping sequence, which is a result of adaptation to downstream gradients in the environment, generally occurring in riverine ecosystems (Statzner et al., 2010). Increasing annual mean water temperature and its range, along with decreasing near-bottom current velocity and decreasing grain size of

bottom sediments are primarily related to differing species traits, such as temperature-dependent respiration, velocity preference or filter-net-building behaviour of species living in different river sections. These traits, in addition, can be strongly linked to the phylogeny of the genus, which indicates the tendency of more frequent downstream evolutionary steps and results in closer phylogenetic relationship of species living closer to each other than those that live further in the sequence from headwaters to estuaries (Statzner & Dolédec, 2011).

The position of the species in the overlapping sequence is more or less restricted, so different stream and river stretches have characteristic species or the combination of them, which—especially in the case of less tolerant, ecologically more demanding taxa—makes them suitable bio-indicator organisms.

Coexistence of species in the overlapping zones of their longitudinal distribution is common and facilitated mostly by partitioning of food supply and net-spinning sites, based on qualitative or spatial differences, as well as on staggering life cycles. Specimens of different species at mutually inhabited sites could also use physical aggression and stridulation for the sake of a successful fight for larval retreats or free net-spinning sites. Exploring and defining the ways and rules of coexistence among hydropsychidaecould help learning the organization and function of community structures.

Deviations from the naturally established sequences and/or assemblages of species, let alone the appearance or expansion of euryecious taxa suggests adverse changes of the stream reach or section in question, including its hydromorphological, physical, chemical or trophic properties, as well as the ecological status of its surroundings. The exact ranges of several physical, chemical and habitat- or landscape-related environmental parameters, preferred by certain species, however, are mostly unknown, and wait for further investigations. Expanding and improving the knowledge about the peculiar and ecologically extremely meaningful longitudinal pattern that the distribution of hydropsychidaee exhibit, identifying the essential habitats of species or discovering the relationship between environmental variables and their distributional patterns not only can forward a better understanding of the underlying processes of stream ecology and riverine ecosystems, but also holds the possibility to use acquired experimental results in

water quality assessment or species distribution modelling (SDM) to investigate, model or forecast how species' distributions can be affected by the changes or alterations in their environment, induced by natural causes, anthropogenic impact or climate change.

Acknowledgements We would like to thank Dr. Arnold Móra and two anonymous reviewers for their valuable comments and suggestions that helped to improve the manuscript.

Author contributions Idea for the article: MF, ZC; Literature research: MF; Writing—original draft preparation: MF; Critical revision: ZC.

Funding Open access funding provided by University of Pécs. MF was supported by the funds and personal grants of the Biology and Sportbiology doctoral programme of the Faculty of Sciences of the University of Pécs, ZC acknowledge funding by the Higher Education Institutional Excellence Programme of the Ministry of Human Capacities in Hungary, within the framework of the 20765-3/2018/FEKUTSTRAT and TUDFO/47138/2019-ITM 'Innovation for sustainable and healthy living and environment' thematic programme of the University of Pécs.

Declarations

Conflict of interest The authors have no conflicts of interest to declare that are relevant to the content of this article.

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