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Title Review on ecological response to hydromorphological degradation and restoration

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Summary

Building on existing data this task further reviewed and analysed the available knowledge on biological responses to hydromorphological degradation and restoration. It went beyond recent projects by especially focusing on the specifics of changes, structures or features determined by hydromorphology and their effects on biota. The main objective was reviewing and compiling the available scientific and grey literature, data and information to analyse the effects of hydromorphological variables and processes on the mandatory biological quality elements of the Water Framework Directive: macrophytes, macroinvertebrates, and fish.

Further objectives comprised i) conceptual considerations and analyses to identify key hydromorphological structures and biological responses to hydromorphological degradation and restoration, ii) identifying principal cause-effect chains for hydromorphology-biota interactions to be used in developing assessment and restoration evaluation tools and to add to the efficiency of measures, and iii) compiling guidance on relevant information.

Key biotic response chains have been developed to very pragmatically simplify the complex interactions between various hydromorphological processes and variables to identify the key mechanisms and effects to which stream biota respond. Coarse gravels maintained by stream power and flow velocity emerged as key indicators for hydromorphological integrity with relevance to the aquatic organisms. Therefore, data exploration and analyses have focused especially on species-specific responses to coarse substrates. Species preferring or depending on such substrates provide specific indicators for hydromorphological degradation, rehabilitation, and integrity.

A second, rather unspecific response to hydromorphology emerged from the limitation of species by stream power, i.e. by physical forces of flows. Indirectly related to that is a positive response of species to habitat diversity and habitat complexity providing shelter from high flow velocities, and resources. River zones integrate over the hydromorphological complexity and habitat complexity within river stretches or water bodies. Thus, species preferences for specific river zones are of indicative value for assessing hydromorphological integrity and have been developed accordingly for European fish species.

Summing up, the effects of hydromorphological changes on aquatic plants, macroinvertebrates and fish have been analysed on the one hand with regard to specific requirements of species as potential sensitive indicators and on the other, with regard to limitations of species due to hydromorphological forces aiming to derive thresholds and boundaries of impacts as well as guidelines for rehabilitation. In addition, potential indicators for the hydromorphological integrity of entire river zones were suggested.

Existing databases (AQEM/STAR, WISER, EFI+) and about 1000 papers and reports on ecological requirements of plants, macroinvertebrates, and fish with relevance to hydromorphology have been reviewed to elucidate specific requirements, preferences, and limitations of, as far as possible, potential indicator species.

The total quantifiable data that it was possible to obtain on species response to hydromorphological changes is rather limited. Of about 500 described aquatic macrophytes species, more than 20,000 freshwater macroinvertebrates, and about 550 lamprey and

fish species, quantitative data on gravel size requirements were found for 10, 56, and 28 taxa, respectively, on flow velocity thresholds for 75, 78, and all fish taxa, the latter derived from regression functions based on total length of fish. However, significant knowledge gaps have been identified regarding the ecological classification and habitat requirements of riverine species which have to be addressed in further field surveys and potentially yield further sensitive indicator species for hydromorphological changes, respectively potential target species for river rehabilitation design and evaluation.

Ecological river region indices seemingly provide a well suited indicator for hydromorphological integrity of river sections or reaches. Highly promising results have been obtained using the Fish Region Index, a fish zonation qualifier which has been implemented and harmonised for 163 lampreys and fish species throughout Europe. First assessments based on the whole sample FRI of a European dataset discriminated hydromorphological impacts very well, especially in larger and lowland rivers. Applicability and sensitivity of this index will be further tested and improved. A comparable index exists for macroinvertebrates but it covers only a rather small selection of the indicator species that may be present.

On-going work comprises the improvement of the newly proposed indices and indicators as well as the derived considerations for efficient river rehabilitation. However, there is still an obvious need for collecting new field data especially addressing the links between hydromorphology and biota identified and conceptualised here.

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1 General objectives

In their River Basin Management Plans (RBMP) 26 Member States have designated altogether 104,311 river water bodies in 157 River Basin Districts (RBD) with a total length of 1.17 million km. About 56% of these water bodies (>51,000) and 64% of their total length (630,000 river km) have been reported to hold less than good ecological status or potential (EEA 2012). Hydromorphological changes have been identified as the most widespread pressure on ecological status of EU waters.

Hydromorphological quality elements comprise the i) hydrological regime, i.e. the quantity and dynamics of flow and the connection to groundwater, ii) river continuity, i.e. longitudinal and lateral migration/movement of fish, migratory species and sediment and iii) river morphology, i.e. the physical habitats, structural complexity, substrate composition, width/depth variation, structure of bed, banks and the riparian zone.

Hydromorphological pressures and altered habitats have been reported from 22 and 16 Member States as the most common pressure and impact for 48.2% and 42.7% of their river water bodies, respectively (Fehér et al. 2012). In Europe more than 30% of the classified river water bodies were affected by flow regulation and 6.8% by water abstraction. The latter was most pronounced in Poland, Bulgaria, Spain and France where >20% of the classified river water bodies were affected by this pressure (Fehér et al. 2012).

By analysing the first RBMPs, EEA (2012) detected a rather weak linkage between status assessment and the definition and implementation of the measures. Although hydromorphological measures have been systematically included in the RBMPs, only half of them indicated specific measures to achieve an ecologically based flow regime, about 40% reported a linkage between water uses, types of hydromorphological pressures and specific hydromorphological measures, and it was generally unclear how the proposed measures are expected to contribute to the improvement of the ecological status or potential (EC 2012). Furthermore, the existing classification of ecological status reported in the RBMPs was of generally low confidence. At the EU level, ecological status has been assessed for 86% of a total of 123,215 river and lake water bodies; however, only one third of them have been classified with medium or high confidence (Lyche-Solheim et al. 2012). The reported uncertainty about the contribution of the proposed measures to the ecological improvement was not surprising (e.g. Kail & Wolter 2011a, 2011b).

Although, in the past an exponentially increasing number of restoration measures have already been implemented to enhance the hydromorphological state of rivers (e.g. Gunkel 1996, Stanford et al. 1996, Cowx & Welcomme 1998, Simons et al. 2001, Buijse et al. 2002, Grift et al. 2003, Bernhardt et al. 2005, Roni et al. 2005, Feld et al. 2006, 2011, Wolter 2010), only very few have been monitored (Bernhardt et al. 2005, Palmer et al. 2005, Roni et al. 2005, 2008, Alexander & Allan 2006, Kail et al. 2007, Jähnig et al. 2009, Wolter 2010, Feld et al. 2011). The evaluated projects further revealed that many measures did not have the desired effects on biota (Brooks et al. 2002, Pretty et al. 2003, Lepori et al. 2005, Roni et al. 2005, Suren & McMurtrie 2005, Jähnig et al. 2009, Palmer et al. 2010) which might relate to inappropriate scale of measure implication or the confounding impacts of multiple stressors at different spatial scales (Sponseller et al. 2001, Weigel et al. 2003, Feld & Hering 2007, Kail & Hering 2009, Miller et al. 2010, Tockner et al. 2010).

Work package 1 (WP1) was drafted in response to the recognized lack of knowledge on the effects of hydromorphological restoration on stream biota. Building on recent attempts to compile existing ecological data (e.g. www.wiser.eu) this task has further reviewed and analysed the available knowledge on biological responses to hydromorphological degradation and restoration. It has gone beyond recent projects by especially focusing on the specifics of hydromorphology, hydromorphological changes and structures, or features determined by hydromorphology and their effects on biota.

The main objective was to review the available scientific and grey literature, and available data and information, and to perform a meta-analysis on the effects of hydromorphological variables and processes on river ecology, in particular the effects on the biological indicators or quality elements (BQE) of the WFD. While the ecological assessment according to the WFD is mandatorily based on phytoplankton, macrophytes, macroinvertebrates and fish, this study considers only the latter three, because phytoplankton does not directly respond to hydromorphology (e.g. Pottgiesser et al. 2008, Wolter et al. 2009, Mischke et al. 2011, Marzin et al. 2012).

The main aim was compiling the available knowledge on quantitative and qualitative relations between hydromorphology and biota as well as the gaps. Further objectives comprised:

- i) conceptual considerations and meta-analyses to identify key hydromorphological structures and effect sizes of biological responses to hydromorphological degradation and restoration,
- ii) identifying the principal cause-effect chains for hydromorphology-biota interactions for use in developing assessment and restoration evaluation tools and to add to the efficiency of measures, and
- iii) compiling guidance on information on the effects of hydromorphological changes of degradation and restoration on the BQEs.

2 Conceptual considerations

With the implementation of the WFD in 2000 a shift in management paradigms has occurred setting ecological status of waters besides a good chemical quality as a mandatory environmental target. With this legacy the Member States adapted to an increasing awareness that, despite measurable, significant success in improvements of water quality and aquatic communities, the trend of declining freshwater biodiversity did not reverse (Aarts et al. 2004, SCBD 2010). Seemingly, mitigating one bottleneck might raise the impact of another.

2.1 *Habitat bottleneck hierarchy*

Significant pressures and impacts reported in the 1st RBMPs (EC 2012, Fehér et al. 2012) have been translated to a hierarchical concept of habitat bottlenecks acting at different spatial and temporal scales comparable to the bio-geographical concept of hierarchical faunal filters (Tonn 1990, Poff 1997, Matthews 1998) (Figure 1).

As far as anoxic conditions have seasonally wiped out most of the non-bacterial aquatic life, reducing inputs and loads of pollutants, in particular of organic materials and nutrients, was the primary objective in river restoration. However, despite the reported progress, diffuse pollution from agriculture and point-source discharges from wastewater treatment plants, industries and the overflow of wastewater from sewage systems still remained as significant pressures in substantial amounts of water bodies (EEA 2012).

The next bottleneck closely interacts with water quality: water quantity. Higher discharges dilute pollutants and lower their oxygen consuming effects, while in contrast, pollutants become more concentrated and their impacts are raised at low discharges. Thus water abstraction which has been identified as a significant pressure in 6.8% of the river water bodies (Fehér et al. 2012) and its mitigation by environmental flow measures might be confounded by water quality pressures again.

Further down the bottleneck hierarchy it becomes substantially more complex if besides water quantity also the flow regime has to be considered. The natural flow regime has five components: magnitude, frequency, duration, timing, and rate of change, which all might become limiting factors next to water quantity. For example, floods reductions commonly simplify both habitat complexity and size, often with additional feedback loops. Summer high flows released by reservoirs enhance vegetation encroachment that changes the habitat structure, size, substrates, and hydraulics.

Restricted connectivity and homogeneous habitats become faunal filters for aquatic communities first if sufficient amounts of water in sufficient physico-chemical quality are available throughout the species' life cycle. At the lowest level of the local stream habitats, the lack of specific substrates might limit the occurrence of specialist species.

Just for completeness: even if all evident hydromorphological bottlenecks have been successfully addressed it might turn out that then other physico-chemical or biological constraints limit further improvement.

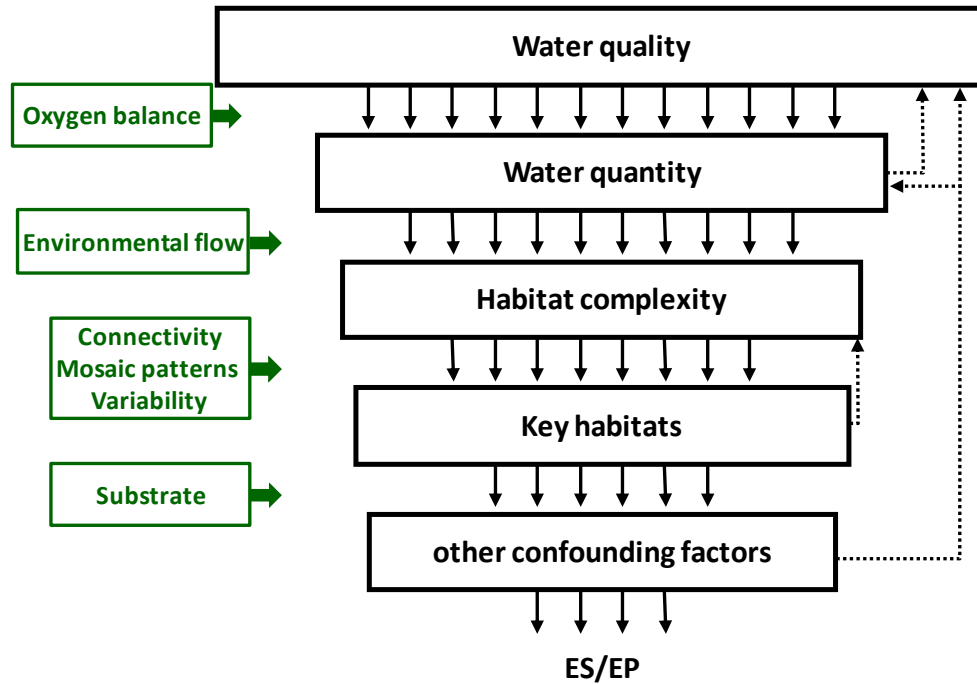


Figure 1 Habitat bottlenecks as hierarchical faunal filters (ES/EP= ecological status/potential; dotted lines indicate feedback loops).

The biological response respectively the restoration success indicated both are highly predictable at the top level and becomes increasingly uncertain at the bottom (Figure 1). There is no doubt about restoration success when any kind of aerobic life boosts after the elimination of temporary anoxia. Sufficient environmental flows become traceable, if fluvial habitats and species assemblages start to develop.

The further degrees of improvement of these riverine communities are much more difficult to assess. Larger and more diverse habitat patches support more species, which generally results in positive empirical relationships between habitat heterogeneity or habitat complexity and species numbers and diversity (Allan 1975, Hugueny 1989, Lake et al. 1994, Rosenzweig 1995, Matthews 1998, Allen et al. 1999, Post et al. 2000, Wolter 2001, Tews et al. 2004, Muotka & Syrjänen 2007, Heino 2009, Passy 2009, Kolasa et al. 2012). Connectivity principally enhances available area and accessibility of different habitat patches and thus, contributes to habitat complexity and heterogeneity. However, the local species diversity strongly depends on the regional species pool and turnover (Ricklefs 1987, Legendre et al. 2005, Heino 2009, Passy 2009, Kolasa et al. 2012); thus, neither the amount of change nor the improvement of specific species or target species can be predicted and related to increasing complexity or heterogeneity of habitats in general (e.g. Palmer et al. 2010).

Therefore, assessments of species response and restoration success have to consider ecoregions, biogeographical differences, and river types and further require a comparative survey design using reference or control sites respectively before/after samplings.

More specific responses or indications have to be expected if certain taxa depend on specific substrates for feeding or spawning and sensitively react on its losses or gains. However, it is inherent in the nature of rivers as disturbance-dominated, dynamic systems

that at this level of microhabitats the number of sensitive indicator species is low and the uncertainty of assessment and prediction high (Figure 1).

2.2 Key biotic response chain

Numerous conceptual schemes have been produced that show the multitude of potential mechanisms, interactions and interrelations between hydromorphological processes and variables at different spatial scales, water chemistry, suspended loads, and biota (e.g. Feld et al. 2011, <http://www.wiser.eu/>). By compiling referenced restoration projects that involved enhancement of instream habitat structures, Feld et al. (2011) produced a conceptual model of in total 64 links between restoration measures, hydromorphological processes and variables, matter retention, nutrient state and the four BQEs of the WFD. Although the single links were supported by studies and empirical evidence, the concerted effect of all possible linkages on biota was very difficult to disentangle and even more difficult to quantify and measure.

Therefore, here a very pragmatic approach has been used to simplify the various interacting hydromorphological processes and variables as much as possible, reducing them to the key mechanisms and effects which structure riverine biota and are, at least to some degree, measurable or assessable in the field (Figure 2). For example, discharge is highly important for maintaining running rivers and mediating connectivity, but species do not directly respond to discharge. They rather respond to flow velocity and drag, or stream power (Statzner et al. 1988, O'Hare et al. 2011).

The main hydromorphological features and structures are primarily determined by the natural flow regime of the river (Poff et al. 1997) and the nature of the sediments available for erosion, transport and deposition. In turn, the interaction between flowing water and the size and quantity of available sediment leads to diverse substrate calibres emerging from flow-induced sorting, which are typical and specific for river systems and thus, indicator for hydromorphological integrity. Accordingly, specific indicator taxa for hydromorphological alterations should respond to these specific substrates, i.e. to coarse gravel, which substantially limits the available number of species and life history traits.

Even if there are several other river types and not all rivers natural gravel-bed rivers, coarse gravel is the only substrate fulfilling both: it requires a significant stream power to be formed and kept clean and a group of specialised species essentially depends on well oxygenated permeable gravel beds for spawning. Therefore, coarse gravel beds indicate hydromorphologically integer river stretches which are directly linked to gravel depending or gravel spawning organisms as biological indicator for high quality gravel beds.

In contrast, typical substrates provided by other than gravel-bed rivers, are either not exclusively found in rivers and formed by stream power, like large wood or sand, and thus, not indicative for hydromorphology, or there are no species specifically responding to, e.g. to bedrock. However, even those non-gravel-bed rivers may host substantial amounts of gravel spawning fish. Fish are mobile organisms which perform more or less distant spawning migrations and as such they are able to use headwater sections for spawning and lower river sections for feeding. The abundance of gravel spawners in other river sections indicates that there is suitable spawning gravel bed somewhere in the catchment as well as sufficient connectivity to it.

The project "Improvement and Spatial extension of the European Fish Index – EFI+" (<http://efi-plus.boku.ac.at/>) has – among others – compiled biological, ecological and life history data as completely as possible for 218 lamprey and freshwater fish species. Just 91 of those species were lithophilic, i.e. gravel spawners with benthic larvae and as such diagnostic for coarse gravels mediated by stream power.

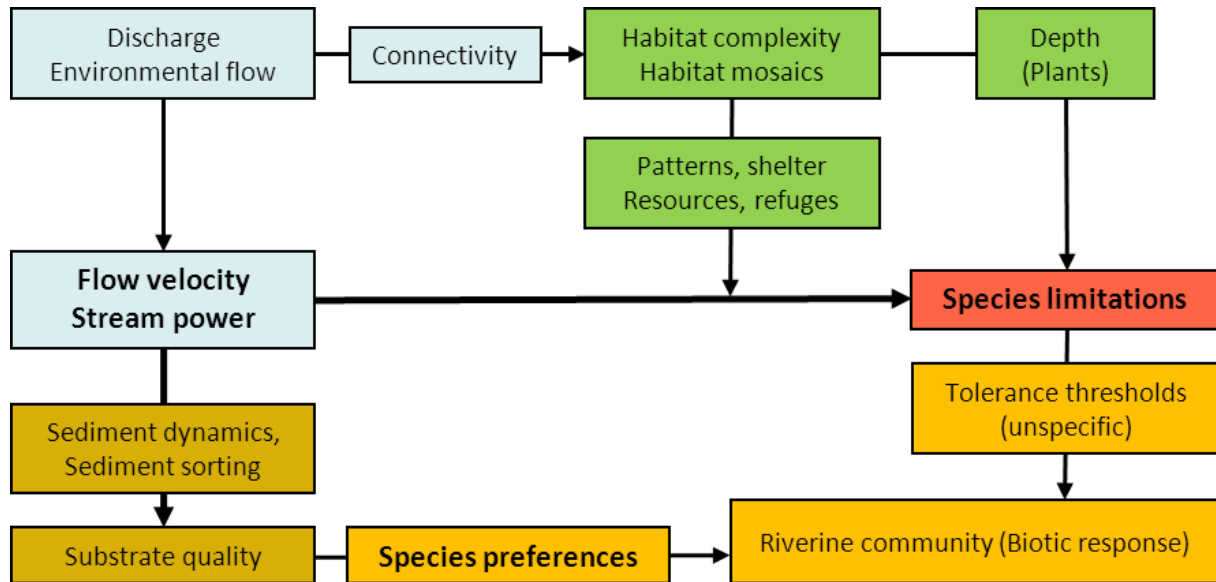


Figure 2 Simplified conceptual flow chart of the basic elements and primary mediator of hydromorphology – aquatic biota interactions in rivers.

Species specialized to woody substrates or plants were considered less diagnostic for hydromorphological integrity, because their requirements could be met in lentic environments too (and often better). If those species prefer lotic environments, their realized ecological niche is most probably not determined by substrate preferences, but by temperature limitations or minimum oxygen requirements instead. That means, even if temperature regime and oxygen availability are substantially influenced by hydromorphology, like turbulent flows, large wood or plant cover, the species do not directly respond to the hydromorphological variables mentioned. For example, of the fish species classified by the EFI+ consortium intolerant against general habitat degradation (66 out of 218) and low oxygen levels (61, which require a minimum of 6 mg O₂/l) only 47 and 39, respectively were lithophilic. Species more sensitive to physico-chemical parameters typically show a less predictable, opportunistic response to the enhancement of hydromorphological habitats.

The limited set of specific indicator species available for hydromorphological integrity might be underlined by the consensus in lamprey and fish species with these three sensitivity traits mentioned. Lithophilic species intolerant of both habitat degradation and oxygen depletion should provide the most sensitive indicator taxa; however, they sum to only 30 species in total, and several of them have very restricted distribution areas: two pure lake species; four non-native salmonids; and very few wide-spread river fishes: trout *Salmo trutta*, salmon *Salmo salar*, grayling *Thymallus thymallus*, brook lamprey

Lampetra planeri, minnow *Phoxinus phoxinus*, spirilin *Alburnoides bipunctatus*, and nase *Chondrostoma nasus*.

A corresponding limitation in numbers of specific indicator species for hydromorphological integrity compared to the total species richness of the taxon was found for aquatic macrophytes and benthic invertebrates as presented later in this report.

The rather unspecific response to hydromorphology is determined by tolerance thresholds of species, age groups and life stages against high flow velocities and shear stresses, which restrict habitat use up to the complete disappearance of species (Figure 2). Common thresholds values of flow velocities reported were <0.3 m/s for species-rich, diverse macrophyte communities (Janauer et al. 2010), 0.3-1.0 m/s for rheophilic invertebrates (Statzner et al. 1988, Söhngen et al. 2008), and 0.1 m/s and 0.5 m/s for hatchlings and juvenile fish, respectively (Wolter & Arlinghaus 2003, 2004). However, these thresholds vary widely within taxa and genera, e.g. between <0.8 m/s, >1.5 m/s and >2.0 m/s for various gastropods, selected dipterids and some beetles, respectively (Statzner et al. 1988). Whilst upper thresholds are exclusive and inversely correlated with the number of resisting species; the provision of low flow habitats <0.3 m/s similarly supports nearly all taxa. In the latter case, it becomes much less predictable which taxa or if the target species will most benefit, because other factors than flow thresholds will determine the success.

Further, with increasing roughness of substrates and banks a wide variety of flow velocities become available in close proximity providing niches for species with highly different flow velocity thresholds. These microhabitat patches are not assessable from average flow metrics nor can the exact position of a sampled specimen within the available flow patterns be recorded in routine surveys.

However, at the level of meso- or macrohabitats these assemblages of microhabitats should become comparable without too much micro-patch detail. The basic idea is that similar river reaches provide similar patterns and combinations of the same microhabitats. Comparable river types or sections show similar assemblages of typical microhabitats, flow patterns and substrate calibres and thus, also similar species assemblages (e.g., Illies 1961, Vannote et al. 1980, Frissell et al. 1986, Statzner & Higl 1986).

The River Continuum Concept (RCC) built on the geomorphological principles proposed by Leopold et al. (1964) which defined a continuous gradient of physical conditions, like width, depth, velocity, flow volume, and entropy gain, from the headwaters to the mouth of any river (Vannote et al. 1980). While these continua broadly exist in natural rivers, they are interrupted by other phenomena (e.g. changes in rock type, tectonic activity, glacial processes) which can disrupt them and cause discontinuities. As a result, the concepts of process domains (Montgomery 1999), and functional process zones, which are ecological communities controlled by the hydrogeomorphic patches (Thorp et al. 2006), have been introduced, and associated with these domains and zones concepts of nested stream habitat hierarchies (Frissell et al. 1986), and ecological patchiness (Statzner & Higl 1986, Poole 2002) are applicable. Accordingly, river systems provide a hierarchical, longitudinal array of functional process zones, which support different styles and dynamics of river channels, with species assemblages equally differentiated from neighbouring, up or downstream communities, based on local processes (Poole 2002, Thorp et al. 2006).

The concept of fish regions to characterize the longitudinal zonation of rivers has been used for more than 100 years (e.g. Frič 1872, von dem Borne 1882) based on the empirical knowledge that the river continuum is a sequence of biocoenotic river regions with distinct fish communities (Thienemann 1925, 1926, Huet 1949, 1953). Later on this fish zonation has been broadened to a more general biocoenotic river characterisation (Illies 1961, Illies & Botosaneanu 1963).

Therefore, the interplay of all flow velocity patterns, habitat complexity, habitat heterogeneity, refuges, shelter, water depth variability, and flow velocity tolerance thresholds of species illustrated in Figure 2 pragmatically refers to a functional process zone sensu Thorp et al. (2006). Species' preferences for such a functional unit could be expressed as a kind of river zonation qualifier indicating which species have to be typically expected in which river regions within the catchment hierarchy (Lasne et al. 2007). In rivers the longitudinal distribution of fish species is an important indicative feature for ecological integrity at the reach scale and beyond. This approach is still in use for fish-based assessments in Austria and Germany (Schmutz et al. 2000, Dußling et al. 2004, 2005).

Summing up the conceptual considerations, the analyses of interactions between hydromorphology and biotic responses of plants, benthic invertebrates, and fish focuses in all taxa on:

- i) identifying sensitive indicators essentially depending on or responding to coarse substrates, which are maintained by stream power showing hydromorphological integrity,
- ii) determining thresholds of physical forces (currents, shear stress, wake wash) which limit habitat use and suitability for species, age groups, and growth forms in plants, and
- iii) improving the indication of complex responses to habitat heterogeneity and hydromorphological integrity at the reach scale by further exploring and improving the concept of river zonation qualifiers.

3 Interactions between hydromorphology and macrophytes

Macrophytes include all higher plants that grow submerged or partly submerged, vascular cryptogams and bryophytes as well as those groups of algae which can be seen as being composed predominantly of a single species (Baatrup-Pedersen et al. 2006). However, macrophyte-based assessments consider hydrophytes, in particular (Meilinger et al. 2005).

The ability of macrophytes to affect the state of a system has long been recognised. A conceptual overview of reported interactions is provided in Figure 3. Since they strongly influence the structure and the ecology of both lotic and lentic ecosystems, many authors refer to them as “biological engineers” (Carpenter & Lodge 1986, Bouma et al. 2005, Cotton et al. 2006, Franklin et al. 2008, Gurnell et al. 2012) and emphasise their importance and role in maintaining ecosystem functioning. Aquatic macrophytes modify their surroundings in a number of ways, e.g. by stabilising the sediment (Hickin 1984, James et al. 2004), altering the flow velocity regime (Marshall & Westlake 1990, Cotton et al. 2006), increasing water depth (Hearne & Armitage 1993), providing substrate and habitat (Flynn et al. 2002, Weber et al. 2012), trapping sediment (Sharpe & James 2006, Wharton et al. 2006), or increasing habitat complexity (Champion & Tanner 2000).

A variety of requirements have to be met for certain macrophytes to appear and persist at a specific site. Principally all macrophytes require elementary nutrients (phosphorus, nitrogen) and light for photosynthesis. Rooting plants additionally require stable sediments. Key factors determining their occurrence and productivity comprise water velocity (Manolaki & Papastergiadou 2013), light (Barko et al. 1986), substrate composition (Baatrup-Pedersen & Riis 1999), nutrient availability (Ibáñez et al. 2012a, 2012b), competition (Flynn et al. 2002), reproduction and dispersal (Barrat-Segretain 1996), and also management practices (Ibáñez et al. 2012a) (compare Figure 3). Many authors refer to flow as one of the key parameters that influence the occurrence and growth of aquatic vegetation (Butcher 1933, Haslam 1978, Dawson 1988, Biggs 1996, Naiman et al. 1999, Strausz et al. 2006). Butcher (1933) pointed out the various factors influencing the distribution of vegetation in moving waters and the differences compared to lentic habitats such as lakes and ponds. More recently, rather basic questions have been considered on how macrophyte assemblages vary naturally in relation to physical parameters (O'Hare et al. 2006), different flow velocities in a single river (Janauer et al. 2010) and among different stream types (Baatrup-Pedersen et al. 2006).

Macrophytes are considered as ecosystem engineers and have accordingly been studied in both views on abiotic factors and processes determining the occurrence, diversity, and distribution of macrophytes (Vermaat & de Bruyne 1993, Riis et al. 2000, Barendregt & Bio 2003, Bernez et al. 2004, Bornette & Puijalon 2011) as well as on how instream (Carpenter & Lodge 1986, Sand-Jensen 1998, Bunn & Arthington 2002, Clarke 2002, Dodds & Biggs 2002, Gurnell et al. 2006, Franklin et al. 2008, Folkard 2011) and riparian vegetation (Corenblit et al. 2007, Gurnell, 2013) affect local hydraulics and sediment dynamics, fluvial landforms, and river channel dynamics.

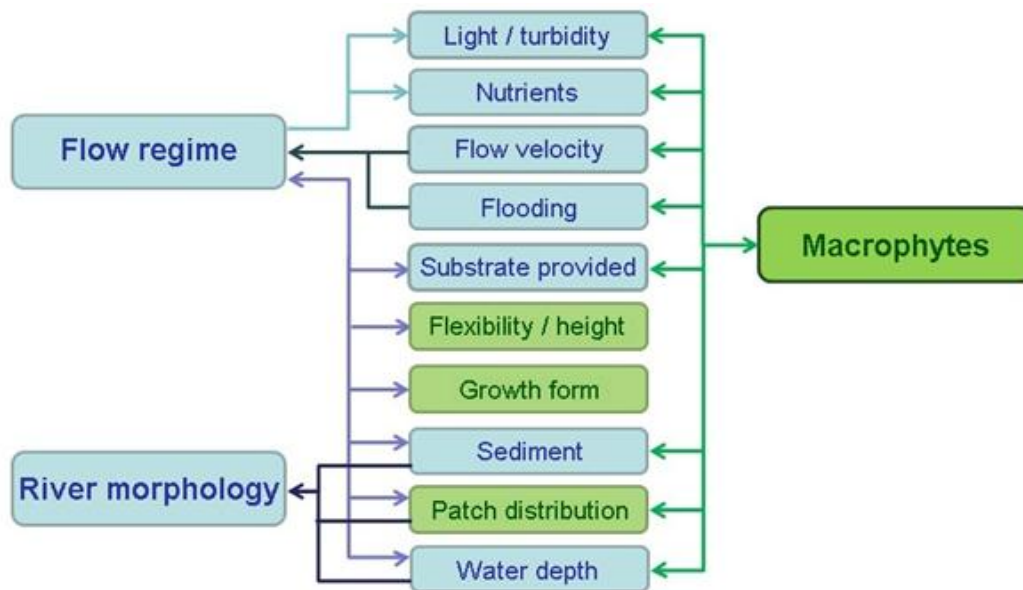


Figure 3 Conceptual overview of interactions between hydromorphology, environmental factors and aquatic vegetation in rivers.

A total of 170 papers have been reviewed to elucidate physical properties, abiotic factors and processes determining the occurrence and distribution of macrophytes in river systems. Data referring to 176 species from all over the world have been compiled. However, only nine species were studied relatively frequently: sago pondweed *Potamogeton pectinatus* (Haslam 1978, Pip 1979, Madsen & Søndergaard 1983, French & Chambers 1996, Pott & Remy 2000, Koch 2001, Hussner & Lösch 2005, Lacoul & Freedman 2006), rigid hornwort *Ceratophyllum demersum* (Haslam 1978, Pip 1979, French & Chambers 1996, Hussner & Lösch 2005, Janauer et al. 2010), arrowhead *Sagittaria sagittifolia* (Haslam 1978, Pott & Remy 2000), Eurasian watermilfoil *Myriophyllum spicatum* (Butcher 1933, Haslam 1978, Barko & Smart 1983, Pott & Remy 2000, Hussner & Lösch 2005, Lacoul & Freedman 2006, Janauer et al. 2010), Canadian waterweed *Elodea canadensis* (Butcher 1933, Haslam 1978, Pip 1979, Barko & Smart 1983, French & Chambers 1996, Pott & Remy 2000, Riis & Biggs 2003, Janauer et al. 2010), stream water-crowfoot *Ranunculus penicillatus* (Koch 2001), floating pondweed *Potamogeton natans* (Haslam 1978, Pip 1979, Hussner & Lösch 2005), European bur-weed *Sparganium emersum* (Haslam 1978, Pott & Remy 2000, Hussner & Lösch 2005), and yellow water lily *Nuphar lutea* (Haslam 1978, Pott & Remy 2000, Janauer et al. 2010). Despite the number of studies dealing with the link between hydrology, biogeochemistry, and biota, only very few have somehow quantified this interaction.

3.1 Interactions between hydrology and instream vegetation

Flow regimes geographically vary in response to climate (precipitation, temperature) and catchment controls on runoff as topography, geology, land cover and position in network vary (Poff & Zimmerman 2010). Headwaters are usually characterised by high altitude, steep slope, high current velocities, and erosion, while lower river reaches are commonly strongly influenced by agriculture and human activities (Barendregt & Bio 2003). In

headwater conditions of fast and turbulent flows even light plays a minor role in determining plant composition (Dawson 1988). Correspondingly, Baattrup-Pedersen et al. (2006) reported an increase in species richness and a transition in plant communities from mosses and liverwort-dominated to vascular plants-dominated when moving from small, shallow mountain streams to middle-sized lowland streams. Provided that there is no limitation of viable seeds and propagules, the hydrological regime of a river is commonly considered the primary control on establishment and success of macrophyte communities (e.g. Butcher 1933, Hudon et al. 2000, Franklin et al. 2008). Other authors further emphasise the importance of flood events and their intensity and frequency as a driving force controlling the colonisation of macrophytes (e.g. Sousa 1984, Resh et al. 1988, Barrat-Segretain & Amoros 1995, Biggs 1996, Strausz et al. 2006, Bernez et al. 2007, Ibáñez et al. 2012a), especially in unshaded streams (Riis & Biggs 2003). Drag has been suggested as the main factor which determines the occurrence of aquatic macrophytes especially in small and shallow rivers, whereas light as limiting factor becomes more important as the water gets deeper and more turbid (Bal et al. 2011b).

Both stimulating and impeding effects of flow on plant growth have been reported. High flow velocities may prevent plant establishment by forming bars of coarse and nutrient-poor sediments, while in contrast, low flow velocities support sedimentation of fine materials resulting in sediments too loose and unstable for anchoring (Madsen et al. 1993). In freshwaters, these physical effects might be superimposed by an inorganic carbon limitation of submersed macrophytes productivity, due to slow CO₂ diffusion rates in water and boundary layer resistance to carbon uptake at leaf surfaces (Barko et al. 1986). Stagnant flow at the boundary layer reduces the transfer rate of carbon and oxygen through the leaf surface, while increasing stream flow velocities will enhance this diffusion rate by reducing the boundary layer thickness (Westlake 1967). Aiming to circumvent limited photosynthesis due to low CO₂ concentrations in the boundary layer, several plant species are capable of utilising HCO₃⁻ instead as their primary carbon source, though (Koch 2001). HCO₃⁻ is much more common in the water column (Sand-Jensen 1983) and can be easily absorbed, e.g., by leaves being polar regarding to pH values as reported for *Potamogeton lucens* and *Elodea canadensis* (Prins et al. 1982). Macrophytes with those properties can therefore maintain photosynthesis more effectively at almost stagnant flow (Koch 2001).

However, slightly enhanced flow velocities promote the growth of aquatic macrophytes due to the previously-mentioned improved diffusion of CO₂ and nutrients (Madsen et al. 2001). An increase in vegetation abundance was evident at velocities up to 0.3 m/s with a peak at about 0.3-0.5 m/s depending on the species (Riis & Biggs 2003). Further increase in flow velocities resulted in reduced plant abundance, mainly due to the increased drag and shear forces (Riis & Biggs 2003). In a northern Swedish stream, Nilsson (1987) studied the distribution of both aquatic and riparian vegetation along a gradient of current velocities and reported linearly increasing species richness of riparian plants with flow velocity while the aquatic species richness peaked at an intermediate flow velocity level. Correspondingly, Janauer et al. (2010) reported plant peak biomass and highest diversity at about 0.3 m/s and the dominance of a few rheophilic mosses at velocities above 0.7 m/s. Several studies have correspondingly shown that flow velocities higher than 0.8 m/s dislodge and eliminate most instream macrophytes (Haslam 1978, Madsen et al. 2001, Strausz et al. 2006, Bernez et al. 2007, Janauer et al. 2010). By studying the impact of artificial floods on stands of *Potamogeton pectinatus* Bernez et al. (2007) found a 40% decrease in plant cover when the discharge was raised from 0.1

m³/s to 0.8 m³/s unfortunately without reporting resulting flow velocities. These results are in agreement with those of Chambers et al. (1991), reporting a decrease in plant biomass and shoot density when mean flow velocities increased from 0.2 m/s to 0.7 m/s. Chambers et al. (1991) also proposed a maximum flow velocity of 1 m/s above which macrophyte growth is negligible or absent. Table 5 summarises the preferred flow velocities of a range of macrophytes found in the literature. As the entirety of biotic and abiotic environmental factors always act together on organisms, those values may differ between the studies cited.

As mentioned before, the metabolic rate of aquatic macrophytes is reportedly linked to the current speed (Chambers et al. 1991, Madsen et al. 1993). However, this linkage depends on factors like nutrient concentration, potential metabolic rate, flow velocity and it is species-specific (Westlake 1967). In a mesocosm experiment, the net photosynthesis rates of *Potamogeton pectinatus* and its associated biofilm were similar at velocities of 0.03 cm/s and 9 cm/s, but gross oxygen production and respiration were about two times higher at the faster flow (Eriksson 2001). Concordantly concerning the higher respiration rates, but contrarily in terms of oxygen production, Madsen et al. (1993) found a 34-61% decline of net photosynthesis and a 2.4-fold increase of dark respiration resulting from an increase in flow velocity from 1 to 8.6 cm/s, examining four different submerged macrophytes under laboratory conditions. Plant species with a high surface-to-volume ratio were more sensitive to flow and therefore, physical stress induced by the constant moving of the plant due to flowing was considered the main reason for this metabolic reaction (Madsen et al. 1993). Champion & Tanner (2000) added the influence of competition on habitat utilisation by plants along a velocity gradient. For example, despite significant signs of stress in *Potamogeton crispus* due to flow velocity – Madsen et al. (1993) reported reduced photosynthesis at 8.6 m/s – this species became most abundant when flow exceeded 0.1 m/s, probably due to the displacement of competitive species (Champion & Tanner 2000).

Other physical forces acting on macrophytes are wind- or vessel-induced waves (Söhngen et al. 2008). For example, young vallisneria plants *Vallisneria spiralis* were found to produce only 50% of the biomass compared to undisturbed plants, when exposed to 0.15 m high waves during an experimental growth period of 67 days (Doyle 2001). At the rivers Spree and Havel in Berlin, large scale reductions of reed belts have been observed due to vessel induced wake wash (Krauß 1992, Heinze & Krauß 2007), with waves >20 cm height already impacting on reed (Sundermeier et al. 2008) further intensified by the abrasive effects of transported solids on stems and periphyton (Ripl et al. 1991).

Stream flow and wake wash do not only directly affect macrophyte growth by physical forces but also indirectly by influencing water's physico-chemistry the physico-chemical properties of the water, such as turbidity, water quality, channel geomorphology or habitat heterogeneity (e.g. James et al. 2004).

3.2 Effects of turbidity and light

The availability of light is one of the key factors regulating the occurrence of aquatic macrophytes (Kautsky 1988, Vermaat & De Bruyne 1993, Köhler et al. 2010) and their distribution within river systems and determining their specific growth form (Hudon et al.

2000). Whilst emerged and floating vegetation expose their leaves directly to the sunlight, the depth distribution of submerged macrophytes is limited by the light absorption of water and phytoplankton (Chambers & Kalff 1985) and attached periphyton (Vermaat & De Bruyne 1993). Light attenuation also results from shading by riparian (Wharton et al. 2006, Köhler et al. 2010) and instream vegetation (Dawson 1976, Sand-Jensen & Borum 1991) as well as changing intensity of solar radiation (Hilton et al. 2006), but also from resuspension of fine sediments and organic materials induced by peak flows (Madsen et al. 2001) or human alterations, in particular by inland navigation (Söhngen et al. 2008).

Euphotic depth and depth distribution of macrophytes are negatively correlated with turbidity. The euphotic depth (T_{eu}) is defined as the depth where the light deficiency limits the photosynthesis by $T_{eu} = 2.709 SD$, where SD is the Secchi depth (in m). The light attenuation coefficient k (m^{-1}) follows $k = 1.7 / SD$ (Giesen et al. 1990).

The impact of turbidity on macrophytes will be most severe at the beginning of the vegetation period, when turbidity substantially restricts the euphotic zone, and thus, the depth range and related area for successful germination and growing of plants, while later in the season periphyton and shading become equally important (Vermaat & De Bruyne 1993).

Mature vallisneria plants exposed to a turbidity of 150 mg l^{-1} TSS (total suspended solids) ceased forming new rosettes and produced significantly less biomass, fewer tubes, and less flowers and seeds than in the control system during a nine week experimental growth period (Doyle 2000). In experiments, at the highest turbidity level of 45 NTU (7% total incident light) the survival of propagules significantly decreased from 50% to 0-17% and 67% to 46% for small buds and seedlings, respectively (Doyle & Smart 2001). In contrast, sago pondweed was less affected indicating a species-specific response to increased turbidity (Doyle 2000). While the turbidity-related impact was most severe at light extinction coefficients below $k = 2.0 \text{ m}^{-1}$, the relative effect declined with further increasing turbidity (Best et al. 2001).

A prolonged and erect plant's growth form enables the specimen to grow faster towards the water surface and thereby lessens the effect of light attenuation. Erect macrophytes and those with floating leaves have a competitive advantage over submerged ones because their growth form allows them to capture light radiations at the surface (Barrat-Segretain 1996). In the littoral zone, common depth distributions of plants range between 1 and 5 m for floating leaved vegetation and up to a maximum water depth of 1.5 m for emerged macrophytes.

Besides the light attenuation by the water column, the epiphytic growth on plant surfaces is another cause of macrophytes' growth restriction due to lowering the incidence of light (Köhler et al. 2010) and the amount of carbon that can be absorbed (Franklin et al. 2008). Flow velocities may affect the growth of those periphytic algae (Wade et al. 2002). Under undisturbed conditions, Flynn et al. (2002) found a positive correlation of seasonal macrophyte growth with periphyton biomass. However, periphyton seemed unable to colonise plants during periods of high flows, which was indicated by overall low periphyton cover at increased discharge (Flynn et al. 2002). Similar observations were made by Strand & Weisner (1996) in different lake systems, where the epiphyton biomass production on *Potamogeton pectinatus* stands was inversely correlated to site exposure. Increasing mechanical forces due to wind-induced waves and currents signifi-

cantly restricted epiphytic growth (Strand & Weisner 1996). In this study, the better light conditions due to the reduced epiphytic cover further promoted *Potamogeton pectinatus* growth and hence led to an increase in biomass production.

Köhler et al. (2010) emphasised that shading by suspended material and epiphytes only matters when light supply is limiting. Under these conditions, the additional shading results in a lower biomass production compared to conditions where light intensity is saturating.

It is remarkable, that once macrophytes are established, their presence may induce a positive feedback (Koch 2001, Hilt et al. 2011). Instream vegetation reduces the flow velocity creating favourable conditions for sedimentation of suspended solids, while reducing erosion and resuspension (Brix 1997). In UK chalk streams dense *Ranunculus* spp. stands with up to 80% coverage significantly reduced flow velocities within the plants and promoted sediment trapping, reaching volumes of 0.085 m³/m² of fine sediment trapped (Wharton et al. 2006). Correspondingly, in a small German creek macrophytes significantly reduced flow velocity and macrophyte biomass was a significant predictor of matter retention, whereas discharge was not (Horvath 2004). A stable submersed macrophyte community, therefore, leads to a lower turbidity value and hence to a higher light penetration within the water column. More light may potentially enable faster growth and a higher final biomass of submersed macrophytes, which may retain even more particles (Köhler et al. 2010). In water bodies where macrophyte distribution is restricted by the penetration depth of light, plants may even increase their own potential colonisation depth due to the increase in water transparency (Kosten et al. 2009). However, especially plants with broader leaves and a more complex growth form may collect larger amounts of silt and mud on their surface, which reduces the quantity of light available to the plant (Haslam 1978).

3.3 Determinants of growth form and height

Water flow determines the vegetation of running waters, governs plant form, dominates the growth-controlling factors and defines the habitats (Dawson 1988). Aquatic plants colonise quite diverse habitats based on structure and physico-chemical conditions (French & Chambers 1996, Koch 2001, Passauer et al. 2002). Accordingly, macrophytes show a variety of morphological adaptations to varying environmental conditions and their competitive abilities are often explained by their growth forms and morphology (Barrat-Segretain 1996). In general, four different growth forms can be distinguished: free-floating, emergent, submerged, and rooted plants with floating leaves (Folkard 2011).

The physical forces acting on flow-exposed plants strongly depend on flow velocity and turbulence (Biggs 1996), but also on several species-specific factors like shoot size, individual roughness, flexibility, and shape (Schutten & Davy 2000). The breakage strength is defined by size and mechanical properties of the stem (Schutten et al. 2005). Generally, plants with high drag coefficients and low anchoring strengths are those species most susceptible to high velocities (Biggs 1996). Therefore, the ability of a plant to tolerate water movement without suffering mechanical damage relies either on minimising the hydrodynamic forces or maximising its breakage and uprooting strengths (Bornette & Puijalon 2011). Environmentally induced variations in morphology were already observed

by Butcher (1933). He suggested that plants in swift rivers must either possess strong stems and leaves as well as efficient rooting systems (e.g. *Ranunculus fluitans*) or exhibit a close cushion-like growth that offers little resistance to the current (e.g. *Eurhynchium ruscifforme*). The leaf and stem morphology as well as the size and rigidity of a plant is a direct response to the flow regime (Bunn & Arthington 2002) and basically represents a trade-off between drag forces and hence mechanical stress acting on the plant and light capture. Hydraulic drag can lead to uprooting (Schutten & Davy 2000) or stem breakage (Brewer & Parker 1990) and has an influence on epiphytic growth and hence light availability (Strand & Weisner 1996, Flynn et al. 2002). The compromise between mechanical stress and light capture is partly apparent in the size of frontal area, planform area and the volume of the canopy relative to the sediment area colonised by plants (Sand-Jensen & Pedersen 2008). In general, increasing leaf area is beneficial for plant photosynthesis but experiences higher drag (Bal et al. 2011a) and makes the plant more vulnerable to high flow velocity conditions. Thin-leaved species usually associated with a high surface to volume ratio are more prone to mechanical action and thus more sensitive to flow (Madsen et al. 1993, Schutten & Davy 2000, Bouma et al. 2005, Sand-Jensen & Pedersen 2008, Bal et al. 2011a, Edmaier et al. 2011). Because a reduction of leaf area results in a lower photosynthetic production, Bal et al. (2011a) compared different macrophyte growth forms in terms of the cost-effectiveness between leaf area and drag forces. At high flow velocities the drag forces on the emergent species *Sparganium erectum* were three to four times higher than on submerged, superficial or floating leaved species leading to the conclusion that the emerged strategy is favoured under low flow conditions, especially since this growth form is not affected by any reduction of light due to the attenuation by the water column (Bal et al. 2011a). Submerged growth was supported by rough conditions and high flow velocities due to the flattening, compressing and reconfiguration of plants which lowered the drag forces (Sand-Jensen 2003, Puijalon et al. 2005, O'Hare et al. 2007, Sukhodolova 2008). Correspondingly, O'Hare et al. (2011) reported fully submerged and flexible *Ranunculus* species still being able to maintain high abundances at a higher level of stream power compared to linear emergent species. An upright posture, maintained by buoyancy and stiffness (Stewart 2006) can be generally found in shallow water following the edge of the channel (Folkard 2011). This elongated growth form is often replaced by flat, rosette-shaped macrophyte species as drag increases (Brewer & Parker 1990, Stewart 2006).

In general, the current acting on macrophytes in streams tends to be unidirectional and constant, thus forces macrophytes to stretch (Madsen et al. 2001). If the flow is steady and unidirectional Sand-Jensen & Pederson (2008) proposed that plants are able to adapt to such conditions by developing the necessary flexibility, strength and overall shape and morphology. A high degree of flexibility allows the plant to be pushed towards the bed into slowly moving water (Stewart 2006), or to be compressed at the bottom to denser stands with higher roughness and lower flow velocities inside (Puijalon et al. 2005, O'Hare et al. 2007, 2011, Sukhodolova 2008), respectively. High current velocity and associated drag should put the canopy in a more slender and compressed shape (Sand-Jensen & Pedersen 2008, Sukhodolova 2008). This streamlining is most pronounced in submerged plant species (Haslam 1978) and both an effect of greater forces exerted on the plant profile and morphogenetic response as the plant grows can be observed (Madsen et al. 2001). In an experimental flume, Schutten & Davy (2000) measured the hydraulic forces acting on shoots of different macrophyte species and found significant correlations between leaf and shoot morphology and hydraulic roughness. They showed that

species with flat leaves and/or two-dimensional architecture (flat shoots) have a significant lower hydraulic roughness than species with round leaves and/or a more extended three-dimensional architecture (Schutten & Davy 2000). Furthermore, their measurements revealed that within each plant group, wide leaves and flexible shoots had a lower hydraulic roughness than narrow leaves and stiff shoots (Schutten & Davy 2000). Similar results were obtained by Miler et al. (2012) investigating four macrophyte species of different growth forms along a velocity gradient. The growth form of water mannagrass *Glyceria fluitans* a semi-aquatic, emerged plant well adapted to low flow velocities, showed a high resistance to breakage and the highest rigidity and stem diameter, whilst the Giant willow moss *Fontinalis antipyretica* showed a high breaking stress and the highest flexibility and appeared to be best adapted to fast flowing waters (Miler et al. 2012). The high flexibility allows the plant to reconfigure and adopt the streamlined shape already mentioned above. Reconfiguration refers to the ability of the plant to adjust its orientation and shape by reducing the cross-sectional area perpendicular to the flow in order to minimise drag (Bouma et al. 2005). However, this capability of reconfiguration to reduce the hydrodynamic forces experienced at high velocities might increase self-shading (Puijalon et al. 2005) and reduce both the photosynthetic surface area and the amount of light received by the leaves (Bal et al. 2011a). Haslam (1978) further showed that streamlined plants are not always the ones with the least resistance. For example, the more bushy growth form of European marshwort *Apium nodiflorum* developing carpets was less resistant than a clump of the streamlined river water crowfoot *Ranunculus fluitans* (Haslam 1978).

A limited number of studies have further investigated intraspecific patterns of adaptive capacities and morphology. For example, the water parsnip *Berula erecta* was found increasing its below-ground biomass with increased flow velocity and minimising drag forces by reducing its size and by shifting from an erect form with one tall ramet to a horizontal form with many short ramets (Puijalon et al. 2005). In contrast, the water mint *Mentha aquatica* increased their above-ground biomass with higher flow velocities, while the below-ground biomass decreased, without any signs of reduction in plant performance along the velocity gradient despite higher drag (Puijalon et al. 2005). The authors explained this finding by an easier reconfiguration of leaves in larger growth forms and by an easier nutrient uptake and gas exchange due to the reduced boundary layer at higher flow velocities. They also stated that the decreased allocation to root biomass and likely increased uprooting risk might be explainable by an improved ability to disperse at high flow conditions.

However, for rooting plants, there is still a need for below-ground adjustments to balance above-ground drag forces (Bal et al. 2011a) and to persist under rough hydraulic conditions. The anchorage strength is defined as the force needed to dislodge the whole plant or to break the roots and depends on age, size and properties of the root system as well on cohesion and mechanical strength of the sediment (Schutten et al. 2005). Since submerged plants are usually dislodged due to uprooting or stem breakage rather than root breakage, Schutten et al. (2005) concluded that roots of aquatic plants have higher tensile strength than their shoots. The risk of becoming uprooted and dislodged is most severe for small and juvenile plants with short and simply branched roots attached to soft sediment and continuously decreases with plant size and increased cohesion strengths (e.g. Haslam 1978, Schutten et al. 2005, Edmaier et al. 2011). Higher plant density further decreases the risk of uprooting since the sediment within plant patches is better protected from erosion (Haslam 1978).

Soft substrates with low cohesion strength are usually inhabited by long-rooting plants like common bur reed *Sparganium erectum* (Haslam 1978, Biggs 1996, Baattrup-Pedersen & Riis 1999, Liffen et al. 2013a, 2013b). In contrast, river sections with consolidated gravel and fast flows are colonised by plants with a tangled, often horizontal root system like *Ranunculus* spp. (Haslam 1978), which increases the stability and the overall resistance of a site (Biggs 1996).

3.4 Effects of nutrients and substrate

Substrate stability significantly controls plant establishment (Franklin et al. 2008) and is largely determined by flow (Haslam 1978). A river bed is highly unstable compared to the bottom of a lake or pond and with increasing amplitude and frequency of water-level changes the ability of plants to permanently root decreases (Butcher 1933). However, a certain degree of natural fluctuations in velocity and water level improves habitat heterogeneity and supports species rich vegetation (Lacoul & Freedman 2006). In a study of Danish streams, the unregulated systems with riffle-pool sections showed a higher percentage of coarse substrates associated with a high abundance of submerged macrophyte species, e.g. *Batrachium peltatum* and *Potamogeton perfoliatus*, while the regulated systems showed high fine sediment coverage associated with emergent macrophytes like *Sparganium emersum* (Baattrup-Pederson & Riis 1999). Table 6 lists preferred substrata of various macrophytes according to different authors.

Flow velocity indirectly shapes the plant community by altering texture and composition of the substrate (Ham et al. 1981, Jowett & Richardson 1989). For example, Chambers & Prepas (1990) reported reduced contents of nutrients, subsoil water and organic matter at exposed sites compared to sediment in sheltered areas. Texture and organic matter content affects the growth rate of macrophytes due to its considerable influence on nutrition (Barko & Smart 1986).

However, whether macrophytes obtain their main nutrients from the substrate or the water column depends on the specific nutrient as well as the plant species in question (Barko et al. 1991). In river systems the likelihood of nutrient limitation is generally low due to a constant input of new drainage water (Riis et al. 2000). Even if easily available, soluble forms of phosphorous (P) and nitrogen (N) in the water usually exist in low concentrations (Barko & Smart 1986). Rooted macrophytes, therefore, use the sediment as primary source for the uptake of nutrients (Barko et al. 1991, Brix 1997). In contrast, floating or drifting plants obtain their minerals mainly from the surrounding water (Butcher 1933). Free-floating plants might be outcompeted by submerged growth forms in areas where nutrient concentrations in the water column are low (Folke et al. 2004). At low flow conditions and high retention time of the water, higher amounts of dissolved nutrients might favour phytoplankton growth to an extent where light supply becomes limiting and euphotic depth decreases, thus excluding submerged plants (Barko et al. 1991).

Chambers et al. (1991) recorded a significant negative correlation between shoot biomass and current velocity. The authors concluded that either higher nutrient concentration in the substrate associated with the sedimentation of smaller particles or increased sediment stability and silt content favour macrophyte growth at low flows. Boeger (1992) suggested a combined effect of both flow velocity and sediment texture on *Ranunculus*

aquatilis L., since it produced the highest amount of biomass on a muddy substrate at whatever velocity. In contrast to this, growing on sand or gravel, growth of *Ranunculus* was generally lower and the extent of the decrease depended on the water velocity. In Eurasian watermilfoil *Myriophyllum spicatum* and hydrilla *Hydrilla verticillata* a 10- and 20-fold decline in growth, respectively, was found with increasing sediment organic matter concentration up to approximately 20% dry sediment mass (Barko & Smart 1986). In this study, poor growth of both species was also obtained on inorganic sediments with a sand content exceeding 75% of dry sediment mass, on dense sandy sediments and on organic sediments of low density. An experimental increase in sediment density with no change in organic matter content stimulated hydrilla growth, indicating that sediment density rather than organic matter content was most influential in regulating growth by determining the nutrient diffusion distances (Barko & Smart 1986). The high rate of microbial degradation and the accompanying production of phytotoxins and lack of oxygen in the proximity of the roots can be another problem for macrophytes growing on organic-enriched substratum (Barko & Smart 1983, Pedersen et al. 2004). However, the roots may counteract the negative impact of the toxins by releasing oxygen (Soana et al. 2012), transported from the shoots through aerenchyma (Moore et al. 1994, Soana & Bartoli 2013). This ability and therefore the extent of the inhibiting effect depend on the species (Sand-Jensen et al. 1982, Raun et al. 2010).

In another study, Nilsson (1987) observed a shift in sediment quality from mainly organic to inorganic at a velocity of 0.3 m/s. This transition at intermediate flow velocity was accompanied by a change in species diversity leading to a peak in species richness at 0.3 m/s. In the Ebro River, Spain, Ibáñez et al. (2012a) reported a dominance shift from phytoplankton to higher macrophytes and suggested that less frequent and less intense flooding due to dam operation have created suitable conditions for macrophytes to establish, although a decrease in phosphorus has likely been the main driver.

Various authors also assume an impact of aquatic vegetation on deposition rates of small particles and the composition of the sediment (Sand-Jensen 1998, Schulz et al. 2003, Sharpe & James 2006). Investigating sedimentation and retention in a vegetated flume, Abt et al. (1994) found those processes to be dependent on the blade shape of *Poa pratensis*, which they used as a model organism with morphology relatively similar to several freshwater macrophytes although it is no aquatic plant.

However, as proposed by Baattrup-Pederson & Riis (1999) the association of different macrophyte species with different substrata might simply occur coincidentally and does not reflect differences in their flow velocity tolerance or the effects of macrophytes on in-stream hydraulics and sedimentation processes.

3.5 Effects of flood frequency

The effect of flooding on vegetation is rather well studied (e.g. Bornette & Amoros 1996, Blanch et al. 1999, Strausz et al. 2006, Bernez et al. 2007, Poff & Zimmerman 2010). The presence and development of macrophytes in lotic systems is primarily controlled by the frequency of high-velocity flood events (Reice et al. 1990, Riis & Biggs 2003). In principal, the degree of disturbance of a plant assemblage by floods is determined by the species-specific growth forms determining their drag properties and rooting strength, by

the age of the community and also by habitat resistance as function of bed stability (Biggs 1996).

Plant communities are well adapted to devastating stochastic flooding extremes by fast regeneration from rhizomes if above-ground parts are heavily damaged or by rapid recolonisation from fragments or fruits (Haslam 1978). However, the timing of a flood event strongly affects the resistance and recovery potential of a plant community, as stated by Madsen et al. (2001). Early in the growing season flood events might simply delay the onset of growth, whereas later in the growing season they might remove substantial biomass and reduce net production (Madsen et al. 2001). Correspondingly, Barrat-Segretain & Amoros (1995) reported a significantly higher effect of a disturbance when the vegetation was at its maximum in summer compared to a disturbance in winter. However, those macrophyte stands disturbed at various seasons similarly recovered in the next spring (Barrat-Segretain & Amoros 1995). Corenblit et al. (2007) distinguished three critical phases when hydrogeomorphic control on vegetation dynamics is particularly strong: (i) reproduction and dispersal of diaspores, (ii) seedling and sapling recruitment, and (iii) adult plant establishment.

Timing and magnitude of flooding not just affects the growth of macrophytes but also the species composition. A more frequently disturbed site is dominated by fast colonising, small weedy species, whereas at rarely disturbed sites slower growing, large species are dominating (Biggs 1996). Frequently and more predictably disturbed communities are expected to be more resilient against flooding than rarely and unpredictably affected ones (Reice et al. 1990). Nevertheless, if the magnitude and frequency of spates exceed a certain threshold, those extreme conditions will cause severe damage to the community. In streams of New Zealand, Riis & Biggs (2003) observed a negative correlation between the frequency of high floods and the abundance and species diversity, as well as varying species compositions at differently disturbed sites.

In the lower Ebro River, Ibáñez et al. (2012b) compared the effects of short (1-2 days) artificial flood pulses with long-lasting (69 days) natural floods on the distribution and abundance of submerged macrophytes and showed a significant reduction of the mean plant cover with the length of flooding time. Therefore, the authors concluded that not just the timing but also the duration of a flooding has a significant effect on the plant community (Ibáñez et al. 2012b).

The recolonisation of a disturbed site by aquatic vegetation depends on the seed input and the germination rates as well as on bed stability (Corenblit et al. 2007). Accordingly, plants with high propagule production constituted a greater proportion of the vegetation in flood-disturbed streams, suggesting that this species trait is important for the maintenance of macrophyte communities in flood-prone streams (Riis & Biggs 2003). However, macrophytes need a rather long period of hydrological stability for successful establishment compared to periphyton and invertebrates (Biggs 1996).

The abundance and diversity of macrophytes was found to decrease as flood disturbance frequency increased by Riis & Biggs (2003) and vegetation was absent in streams with more than 13 high-flow disturbances (defined as seven times the median flow) per year. Still, a frequency of eight flood events per year resulted in significant declines of plant biomass (Riis & Biggs 2003). In corresponding flume experiments, uprooting associated with bed sediment erosion rather than stem breakage has been identified as the primary mechanism at high water velocity (Riis & Biggs 2003).

Although high flow events often have damaging effects on the plant community, they may also promote their growth and distribution, e.g. by facilitating colonisation and re-distribution of plant fragments or seeds, or by favouring the establishment of new pioneer species (Corenblit et al. 2007). Depending on the magnitude, flood may become beneficial for certain species due to the removal of fine sediments without disturbing the coarse bedload (Reice et al. 1990).

Therefore, flood events, and disturbances in general, are a source of heterogeneity in the structure and dynamics of natural assemblages (Sousa 1984) and together with interspecific competition and phenological cycles proposed to be the primary factors controlling seasonality in macrophyte growth and abundance (Champion & Tanner 2000).

4 Effects of hydromorphology on benthic invertebrates

Benthic invertebrates are the most widely used organisms in freshwater biomonitoring of human impacts (Bonada et al. 2006). However, this monitoring rather shifted from assessing impacts of organic pollution towards to those of altered hydraulic and physical habitat characteristics (e.g. Dolédec et al. 2007, Pedersen & Friberg 2009). Until now, most studies separately analyse the impacts of hydrology or morphology on benthic invertebrates, thereby neglecting the influence of interactions between both effects. There is still a considerable lack of knowledge on how hydromorphological impacts are in detail linked to instream-responses of specific species. This lack of knowledge has supported studies that investigate how local habitat features influence benthic invertebrate communities under changing river discharge (Dunbar et al. 2010). Such research might advance conceptual understanding of invertebrate responses from flow response guilds to habitat response guilds (Arthington et al. 2010); however, uncertainties in knowledge of the mechanistic pathways of those responses still persist.

Numerous habitat requirements of benthic invertebrates have been compiled within European funded projects like STAR and WISER and went into assessment schemes like ASTERISCS with modules on hydromorphology, general degradation, and river zonation. Therefore, this review has in particular focused on available information on physical thresholds for flow velocity and shear forces respectively suitable or tolerable sediment calibre as input for river rehabilitation planning.

4.1 Role of complexity and heterogeneity of physical habitats

The composition of the substrate influences benthic invertebrate communities and certain species show substrate preferences or avoidances (Angradi 1999, Buss et al. 2004, Waters 1995). The quality and quantity of organic matter in the sediment and the stability of the substrate can alter benthic invertebrate communities (Buss et al. 2004, Jowett 2003), but also the chemical composition of fine sediment (Von Bertrab et al. 2013). Thereby, water flow is the primary driver that determines substrate particle size and subsequently the presence of flow refuges or food sources in interstitial spaces. Sand is a very instable habitat and sandy sediment particles and organic matter are easily eroded by higher flows making sand habitats not as suitable for benthic invertebrates as other habitats (Allan & Castillo 2007). The richness of Ephemeroptera, Plecoptera and Trichoptera (EPT) species was found to be influenced by the available substrate type (Timm 2003) and to be lower in sandy than in harder substrates (Timm et al. 2008). Similarly, Maxted et al. (2003) found that half of all taxa and one third of the EPT taxa are commonly missing on sandy bottoms compared to rocky substrates. In another study by Pan et al. (2012), sediment beds containing larger particle sizes such as gravel or cobble provided more stable microhabitats and supported higher numbers of taxa than sandy sediment beds; but also organic-rich sediments sustained large numbers of invertebrates (i.e. oligochaetes and chironomid larvae). Therefore, sediment beds with greater particle sizes can create high quality habitat environments for benthic invertebrates in contrast to sand sediment beds of smaller particle sizes (Duan et al. 2009). Such patterns of benthic invertebrate distribution and abundance have also been reported previously (Beauger et

al. 2006, Reice 1980) and strengthen the value of a diverse habitat heterogeneity for benthic invertebrate communities (Buss et al. 2004).

Substrate size has been shown to consist a significant predictor of benthic invertebrate diversity (see references above, Culp et al. 1983, Death 2000, Gore et al. 2001, Minshall 1984, all cited in Jowett 2003), but in particular a high surface complexity of the substrate particles is associated with a high species richness (see e.g. review by Minshall 1984). This pattern of benthic invertebrate distribution is not only found specifically for substrate particles, but also in other habitat types (such as woody debris or macrophytes) in general. Additionally, complex habitat types provide patches of high species richness in streams with less complex surrounding habitats such as sand beds (Rader & McArthur 1995). In Australian lowland streams an increasing species richness of benthic invertebrates with habitat complexity has been shown by analysing the colonization of artificial snags of different complexity (O'Connor 1991). Moreover, on the analysed snags, different species groups selected different microhabitats, which seemed related to altered levels of sediment deposition between the different types of complexity (O'Connor 1991). Finally, it was shown that the species richness on snags is higher compared to the surrounding benthos, due to the higher level of dissolved oxygen in this habitat (O'Connor 1991). These findings of O'Connor (1991) have been supported by a recent study of Graeber et al. (2013) showing the cascading effects of flow reduction and resulting dissolved oxygen depletion in altering the benthic community structure in lowland rivers. Another study of Entrekin et al. (2009) showed that wood addition considerably enhanced secondary production in Michigan streams. While benthic invertebrate structure in areas without wood (the main channel) was driven by substrate composition, benthic invertebrate secondary production increased with wood addition due to the retention and accumulation of leaf litter.

Wood and woody debris provide not only important food resources for grazer and shredder by the retention of organic matter (Wondzell & Bisson 2003), it also acts as a food source itself for many facultative and obligate xylophagous benthic species as well as physical habitat (reviewed by Hoffmann & Hering 2000). The local changes in sediment grain size and organic matter content caused by wood assemblages therefore offer a huge variety of meso- and microhabitats for benthic invertebrates. A detailed list of wood associated invertebrate species has been recently compiled by Hoffman & Hering (2000) and Godfrey (2003). Both studies highlighted the ecological value of wood assemblages for benthic invertebrates, Strayer & Findlay (2010) in particular the importance of dead wood in the shore zones. Wood increases the available surface for benthic invertebrate species (e.g. for sessile mussel taxa) and microbial biofilm, with the latter providing the trophic basis for the littoral food web and further invertebrate assemblages. Additionally, major accumulations of wood are able to protect shorelines from erosion or wave action (Gurnell et al. 2005, Piégay 2003, both cited in Strayer & Findlay 2010), causing hydraulic stresses to benthic invertebrates at lower levels than without wood assemblages. Hence, wood assemblages can massively positively impact benthic invertebrate communities and species diversity (Benke & Wallace 2003, Wondzell & Bisson 2003).

Benthic invertebrates particularly profit from complex habitat structures such as wood in areas where other structures are not available (Strayer & Findlay 2010) and community composition is driven by substrate composition (Entrekin et al. 2009). Submerged macrophytes increase the habitat complexity for benthic invertebrates similarly to large wood (Armitage et al. 1995, Kovalenko et al. 2012). This macrophytes-based increase in com-

plexity yields benthic invertebrates assemblages within macrophytes stands which substantially differ from those of silt, sand or gravel substrates (e.g. Armitage et al. 1995). In addition, the increase in habitat complexity due to different macrophytes structures and growth forms can lead to higher species richness. For example, Taniguchi et al. (2003) demonstrated a positive relation between the complexity of macrophytes habitats and the number of macroinvertebrate taxa on both natural and artificial macrophytes. Corresponding to the colonization of snags by benthic invertebrates (O'Connor 1991) it has been concluded that neither increased habitat area nor food resources caused the higher taxa richness of complex habitats (as e.g. suggested by Jeffries 1993), rather than the heterogeneity of the available habitat (Taniguchi et al. 2003).

4.2 Invertebrate's substrate preferences

As outlined above, the presence of benthic invertebrates is especially determined by the composition of the substratum. However, these substrates do not provide homogeneous environments for benthic invertebrates; at very small spatial scales they are rather patchily structured. This characteristic and the high mobility of benthic invertebrate species hamper the identification of species related substrate preferences. Further, it has been shown that substratum size is not as useful in describing physical habitat characteristics at the micro-scale of 0.1-1.0 m² as commonly believed, because the size distribution of substratum within a reach often reflects a past flow spate rather than present flow conditions (Resh 1979, Resh et al. 1988). Nevertheless, a number of studies related the presence of invertebrate species to preferable substrates and substrate grain sizes (Tolkamp 1980, 1982, Singh et al. 2010). Those studies calculated on the basis of substrate classes the index of representation (IR) as a quantitative measure of invertebrates' substrate preference (Hildrew & Townsend 1976). Positive IR values indicate a more than average representation (preference) of a species within a certain substrate class, negative a below average, i.e. avoidance.

However, detailed information on preferred grain sizes is widely lacking for invertebrates and commonly reduced to a more general habitat description (e.g. lithal, macrophytes, particulate organic matter, woody debris). Therefore, substrate requirements have been reviewed and a data set compiled of sediment and grain size preferences for in total 72 and 60 invertebrate species, respectively (Table 7 in the Appendix). IR values of species studied by Tolkamp (1982) and Singh et al. (2010) have been associated to the respective Phi indices of the investigated substrate classes and converted to grain size fractions according to Tolkamp (1980).

Especially the study by Singh et al. (2010) revealed that the benthic invertebrate community changed seasonally over time, which is related to changes in the substrate (caused by e.g. changes in flow), but might be also caused by additional ecological effects. Remarkably, species prefer coarser substrates during summer periods and finer substrates during winter. The fine substrate is washed away after rainfall events in spring and summer and the remaining coarse bed material provides well oxygenated environments, which probably drives invertebrates to actively select such favourable habitats (Singh et al. 2010, Tolkamp 1980). Tolkamp (1982) also pointed out that the substrate preference of invertebrates is related to their feeding habitats and food preferences. As an example, Table 1 summarizes the habitats preferred by four functional feeding groups in two streams (Tolkamp 1982, 1980).

Table 1 Substrate preferences of selected invertebrates' feeding types in two differing streams (Snijdersveerbeek, Ratumsebeek) according to Tolkamp (1980, 1982); BS= bare sand, BG= bare gravel, S= sand, G= gravel, D= detritus, FD= fine detritus.

Feeding type	Substrate type	
	Snijdersveerbeek	Ratumsebeek
Predators	S+FD, S+D, S+D+FD, G+D/FD, D/FD	S+D+FD
Scrapers/Grazers	BS, BG, G+D/FD	BS, BG, G+D/FD
Shredders w/o <i>G. pulex</i>	D/FD	D/FD
Shredders w/o <i>G. pulex</i> , <i>N. cinerea</i>		S+D, D/FD
<i>Gammarus pulex</i>	S+D, D/FD	D/FD
<i>Nemoura cinerea</i>		BG, D/FD
Collectors w/o <i>M. gr. praecox</i>	S+D, S+D+FD, G+D/FD, D/FD	S+D+FD, D/FD
<i>Micropsectra gr. praecox</i>	S+FD, S+D+FD, D/FD	S+D+FD, D/FD

From the analysis of micro-distribution of functional feeding groups in stream ecosystems, Tolkamp (1982) concluded that i) predators occur in all substrate types except for simple mineral substrates, ii) scrapers and grazers on gravel and sand due to their food preference for biofilm, iii) shredders prefer habitats with adequate supply of organic material and detritus, and iv) collectors in mineral substrates providing a suitable amount of detritus. Subsequent studies confirmed this pattern and further figured out that larger substrates offer not only better food resources for biofilm grazers and scraper but also for shredders and collectors by trapping particulate organic matter (Allan & Castillo 2007, Culp et al. 1983, Williams & Moore 1986). Invertebrates' active choice of suitable habitats suggests that they are able to cope with a broad range of substrate sizes and that their occurrence is not exclusively controlled by substrate composition but by its interaction with other environmental factors (Jowett 2003).

4.3 Invertebrate's hydraulic habitat preferences

The physical habitat of benthic invertebrates is strongly determined by the surrounding hydraulic environment influencing their distribution (e.g. Hart & Finelli 1999, Jowett 2003) and community composition (Gabel 2012). Various hydraulic variables have been studied to describe near-bed hydraulic conditions and to predict invertebrates' habitat use, like flow velocity and water depth (Jowett 1989, Milhous et al. 1989), their interactions with substrate variability (e.g. Jowett & Richardson 1990, Quinn & Hickey 1994, Statzner et al. 1988), Froude number, shear velocity, and shear stress (Gore 1996). In particular, bed shear stress performs well in predicting the occurrence of benthic invertebrates, because it accounts for the turbulences at the bed surface generated by sediment roughness which create drag and lift forces acting on benthic invertebrates (Mérigoux & Dolédec 2004, Möbes-Hansen & Waringer 1998). Bed shear stress calculations incorporate three-dimensional measurements of longitudinal, vertical and lateral flow velocities as well as sediment bed structure and are able to discriminate between laminar, smooth

turbulent or rough turbulent flows (see e.g. Soulsby (1997) for description of bed shear stress calculations).

Many studies have applied different variables to describe the key hydraulic preferences of benthic invertebrate species (Statzner et al. 1988) which makes direct comparisons between investigations difficult or impossible. Hence, Statzner & Müller (1989) presented a standardized method to describe the complex hydraulic conditions at the local scale in a very simple and easy applicable way. They developed standard FST (FließwasserStammTisch) hemispheres of identical size but different densities to be exposed on a horizontal plane at the stream bottom. The near-bed flow conditions can then be characterized by the heaviest hemisphere that is moved by hydraulic forces. Nevertheless, this integrated measure of local hydraulic conditions by Statzner & Müller (1989) provides a new variable hardly comparable with previous estimates of hydraulics, although calibrations against key hydraulic characteristics are provided. Thus, FST hemispheres have been finally calibrated in a laboratory flume using commercial hemisphere equipment (Statzner et al. 1991). This improved laboratory calibration of FST hemispheres enabled a close approximation of flow forces near the bottom sufficient to be used in river ecology.

Recent modelling approaches use mean FST hemisphere values to describe the hydraulic preferences of aquatic organisms such as benthic invertebrates (Dolédec et al. 2007, Méricoux et al. 2009). By using near-bed hydraulics derived from FST hemispheres, Dolédec et al. (2007) and Méricoux et al. (2009) characterized the hydraulic preferences of 151 benthic macroinvertebrate taxa collected in German streams respectively of 66 species collected in French Rivers. In total, both studies provided average hemisphere numbers for 181 benthic invertebrate taxa.

This meta-analysis has converted the hemisphere numbers determined for the invertebrate species to shear stress after Statzner et al. (1991) to obtain their shear stress preferences describing their favoured hydraulic habitat (Table 8). Additional information on ecological requirements especially on current preference of invertebrates has been reviewed using the AQEM/STAR macroinvertebrates database (Schmidt-Kloiber & Hering 2012) and additional scientific literature. The presented data compilation is the first comprehensive summary of preferred shear stress environments of benthic invertebrates comprising taxa from 61 families. The FST hemisphere values were obtained from rivers and streams of different size, which might hamper the transferability of the hydraulic preferences to other regions. This problem was discussed in more detail by Lamouroux et al. (2012); however, the presented results still indicate a transferability of the hydraulic habitat preferences obtained to other regions.

4.4 Resistance to increased flow velocity and shear stress

Benthic invertebrate drift is well reported to increase with increasing discharge and flow velocity. Thereby, the number of individuals in the drift is highest in the first minutes of discharge or flow velocity increase and then slowly returns to the baseline drift level, even under increased hydraulic stress conditions (Bruno et al. 2010, Imbert & Perry 2000, Mochizuki et al. 2006, Robinson et al. 2004). Most studies related the response of benthic invertebrates to the maximum increase of flow velocity and discharge, or the duration of base and peak flows (e.g. Gibbins et al. 2010, Minshall 1988, Mochizuki et al. 2006, Wilzbach et al. 1988). Nevertheless, habitat preferences have also been shown

influencing drift responses (Holomuzki & Biggs 2000). Additionally, body shape and behaviour of invertebrates cause significant differences in drift responses to hydraulic stress leading to changes in the composition of the drifting invertebrate community over the duration of high flow events (Bruno et al. 2010, Hart & Finelli 1999, Holomuzki & Biggs 2000, Jakob et al. 2003).

Despite the well-known and frequently shown positive relation of increasing flow velocity/discharge and invertebrates drift, only few studies provide minimum flow velocities or velocity thresholds causing detachment or dislodgement of benthic invertebrates (e.g. Dorier & Vaillant 1954, Holomuzki & Biggs 2000, Statzner et al. 1988, Wilzbach et al. 1988). As outlined above, critical flow velocities to dislodge benthic invertebrates can considerably vary with body shape, but also with body size. Bigger specimens are typically more powerful to actively resist hydraulic forces than smaller or juveniles. Therefore, preferred or threshold flow velocities commonly refer to adults of average size. In addition, flow velocity measurements accompanying invertebrates' sampling are often point measurements at certain water depths or depth averaged. Thus, such measurements rarely represent the real critical flows acting on benthic invertebrates at the substrate, but they provide rough estimates and also general insight to dislodgement behaviours of taxa.

The available literature has been reviewed to provide average flow velocities necessary to detach or dislodge invertebrates (Table 2).

Table 2 Critical flow velocities (V_{crit} m/s) reported to detach and dislodge benthic invertebrates.

Species	V_{crit}	Ref.	Species	V_{crit}	Ref.
Crustacea					
<i>Asellus aquaticus</i>	0.70	1	<i>Bithynia tentaculata</i>	0.82	1
<i>Gammarus fossarum</i>	0.19 – 0.38	4	<i>Bulinus jousseaumei</i>	0.86	2
	>0.30	5	<i>Lymnaea stagnalis</i>	0.70	2
<i>Gammarus pulex</i>	0.99	1	<i>Lymnaea stagnalis</i>	0.75	1
Coleoptera					
<i>Agabus biguttatus</i>	1.32	1	<i>Physa fontinalis</i>	0.66	2
<i>Helmis</i> sp. (l)	2.16	1	<i>Physa fontinalis</i>	0.89	1
<i>Hydrocyphon australis</i>	1.91	1	<i>Physella propinqua</i>	0.84	7
<i>Latelmis surcoufi</i> (a)	0.54	1	<i>Planorbis planorbis</i>	0.86	2
<i>Psephenus</i> sp.	0.71	3	<i>Radix limosa</i>	2.02	1
			<i>Radix peregra</i>	0.86	2
			<i>Stagnicola palustris</i>	0.80	7
			<i>Theodoxus fluviatilis</i>	2.4	1
Diptera					
<i>Cardiocreps brevisrostris</i>	>2.40	1	Hirudinea		
Chironomidae	ca 0.095	6	<i>Glossiphonia complanata</i>	2.4	1
Chironomini sp.	ca 0.05	3	<i>Haemopsis sanguisuga</i>	2.4	1
<i>Eukiefferiella coerulescens</i>	>2.40	1	<i>Herpobdella octoculata</i>	2.4	1
<i>Liponeura cinerascens</i>	>2.40	1	Odonata		
<i>Prosimulia</i> sp.	ca 0.71	3	<i>Aeshna cyanea</i>	0.27 – 0.38	8
<i>Heptagyia punctulata</i>	>2.40	1	<i>Agrion</i> sp.	0.77	1
<i>Simulium ornatum</i>	2.40	1	<i>Calopteryx</i> sp.	0.77	1
<i>Tipula</i> sp.	ca 0.03	3	<i>Somatochlora flavomaculata</i>	0.33	8
Ephemeroptera					
	0.5	10	Oligochaeta		
				ca 0.095	6

Species	V _{crit}	Ref.	Species	V _{crit}	Ref.
<i>Baetis gemellus</i>	2.40	1	Plecoptera		
<i>Baetis rhodani</i>	1.77	1	<i>Chloroperla</i> sp.	>2.40	1
<i>Chloeon</i> sp.	0.60	1	<i>Dinocras cephalotes</i>	2.40	1
<i>Ecdyonurus</i> sp.	2.12	1	<i>Nemoura cinerea</i>	0.30	9
<i>Ecdyonurus venosus</i>	1.65–2.0	13	<i>Perla marginata</i>	1.86	1
	1.54	1	<i>Protoemura</i> sp.	1.98	1
<i>Epeorus assimilis</i>	>2.40	1	<i>Taeniopteryx</i> sp.	0.65	3
<i>Epeorus alpicola</i>	>2.40	1	<i>Tallaperla</i> sp.	0.52	3
<i>Heptagenia lateralis</i>	1.88	1	Trichoptera	> 1.00	10
<i>Isonychia</i> sp.	0.71	3	<i>Agapetus numidicus</i>	0.89	1
<i>Paraleptophlebia</i> sp.	0.71	3	<i>Drysus annulatus</i>	1.72	1
<i>Paraleptophlebia</i> sp.	1.01	1	<i>Drysus</i> sp.	1.66	1
<i>Rhithrogena semicolorata</i>	1.82	1	<i>Goera pilosa</i>	1.32	1
<i>Serratella ignita</i>	0.10	12	<i>Hydropsyche</i> sp.	1.93	1
<i>Stenonema</i> sp.	0.71	3	<i>Odontocerum albicorne</i>	1.03	1
Gastropoda	0.4	10	<i>Rhyacophila</i> sp.	2.00	1
<i>Ancylus fluviatilis</i>	2.4	1	<i>Tinodes algerica</i>	2.25	1
<i>Ancylus capuloides</i>	0.65	1	Turbellaria		
<i>Anisus vortex</i>	0.86	2	<i>Planaria alpina</i>	1.43	1
<i>Biomphalaria glabrata</i>	0.65	14	<i>Dendrocoelum lacteum</i>	0.76	1
<i>Biomphalaria glabrata</i>	0.33	11	<i>Dugesia gonocephala</i>	1.25	1
<i>Biomphalaria glabrata</i>	0.86	2	<i>Polycelis felina</i>	0.99	1
			<i>Polycelis nigra</i>	0.37	1

Ref.: 1= Dorier & Vaillant (1954), 2= Dussart (1987), 3= Wilzbach et al. (1988), 4= Franke (1977), 5= Scherer (1965), 6= Palmer (1992), 7= Moore (1964), 8= Blanckaert et al. (2012), 9= Bengtsson (1984), 10= Holomuzki & Biggs (2000), 11= Madelin (1984), 12= Butz (1973), 13= Butz (1979), 14= Jobin & Ippen (1964).

Critical flow velocities detaching and dislodging invertebrates are typically much higher than the preferred flow velocities in their natural habitats (Table 3). However, data illustrated by Söhnngen et al. (2008) indicated a surprisingly high ability to move against flow velocities close to the detachment threshold for a number of species (Table 3).

Correspondingly, in German waterways, field measurements performed by the Federal Institute of Hydrology during benthic invertebrates monitoring programs recorded a broad variability in measured maximum flow velocities tolerated by individual taxa resulting in a broad range of optimum flows (Figure 4). The broadest range was realized by rheophilic species covering patterns up to 1 m/s, while limnophilic species prefer substantially lower flows of less than 0.2 m/s. Rheobiont macroinvertebrates preferring flow velocities > 1 m/s are rather scarce in large rivers (Figure 4).

Table 3 Flow velocities (m/s) and the presence of stream benthic invertebrates (data according to Dorier & Vaillant 1954 and Söhngen et al. 2008).

Species	Field measurements at sampling location		Experimental observations	
	max	min	Max. velocity allowing for upstream migration	Velocity leading to downstream displacement
Turbellaria (flatworms)				
<i>Crenobia alpina</i>	0.14	0.10	1.40	1.43
Gastropoda (snails)				
<i>Ancylus fluviatilis</i>	0.24	0.10	1.09	2.40
<i>Theodoxus fluviatilis</i>	0.78	0.10	1.09	2.40
Ephemeroptera (mayflies)				
<i>Heptagenia lateralis</i>	0.28		1.40	1.88
<i>Baetis gemellus</i>	1.82	0.10	1.87	2.40
<i>Epeorus alpicola</i>	2.22		2.40	2.40
Trichoptera (caddisflies)				
<i>Rhyacophila</i> sp.	1.25		1.00	2.00
Diptera (true flies)				
<i>Simulium omatum</i>	1.14	0.41	1.17	2.40
<i>Liponeura cinerascens</i>	2.20		2.40	2.40

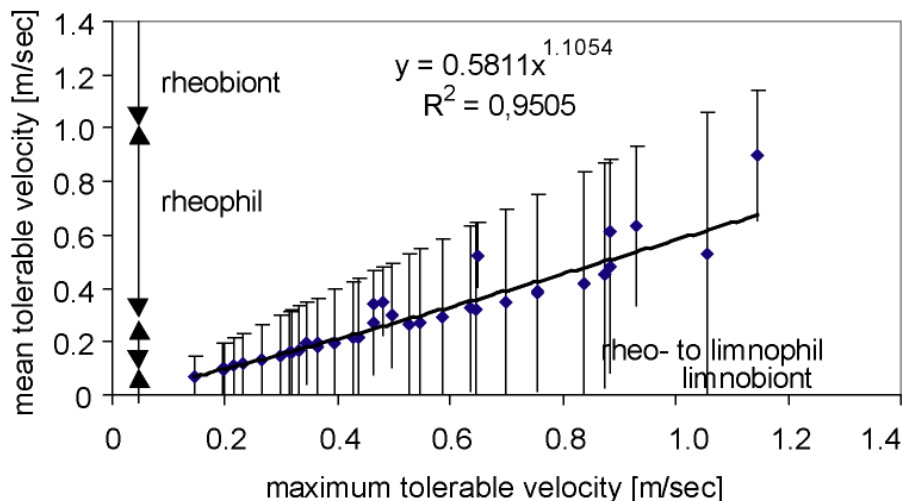


Figure 4 Optimum flow velocities of different invertebrate taxa in large German rivers (from Söhngen et al. 2008).

Shear stresses near the sediment more precisely predict hydraulic condition benthic invertebrates experience in their hydraulic environment (Möbes-Hansen & Waringer 1998). Therefore, in addition available data have been compiled on average shear stress necessary to detach and dislodge invertebrates (Table 9). Only six studies have been identified providing data on tolerated shear stress for 27 taxa, which additionally considered varying body size (Hauer et al. 2012, Schnauder et al. 2010) or the source habitat where individuals experience the moment of the drift causing event (Borchardt 1993, Gabel et al. 2012). For 14 of these 27 species data were available on both hydraulic preferences and critical shear stresses. While as expected most of the species are subjected to higher shear stresses for dislodgement than they hydraulically prefer, the opposite was reported for the caddisfly *Rhyacophila* spp. and the mayflies *Epeorus sylvicola* and *Rhithrogena semicoloranta*. These species obviously prefer hydraulic habitats of higher shear stress than the critical shear stresses for dislodgement observed. However, while hydraulic preferences of these species were derived from sampling in the large Upper Rhône River (France) (Mérigoux et al. 2009), their critical shear stress thresholds have been determined using individuals sampled in the small Ybbs River (Austria) (Hauer et al. 2012). Correspondingly, Mérigoux et al. (2009) has shown variations in hydraulic preference of species due to river size by comparing hydraulic preferences of 32 taxa with such derived by Dolédec et al. (2007) for the same species. Similarly, Hauer et al. (2012) obtained a critical shear stress threshold of 0.26 N/m² dislodging individuals of the mayfly *Baetis* sp., while Gibbins et al. (2010) reported 9 N/m² and further noted little drift of *Baetis* below this threshold of 9 N/m². The high critical shear stress thresholds reported for these mayfly taxa might be related to the interaction of increasing flow velocity and bed instability. The species might have profited from low flow refuges at and within the coarse sediment structure leading only to drift responses when the refuges are washed away.

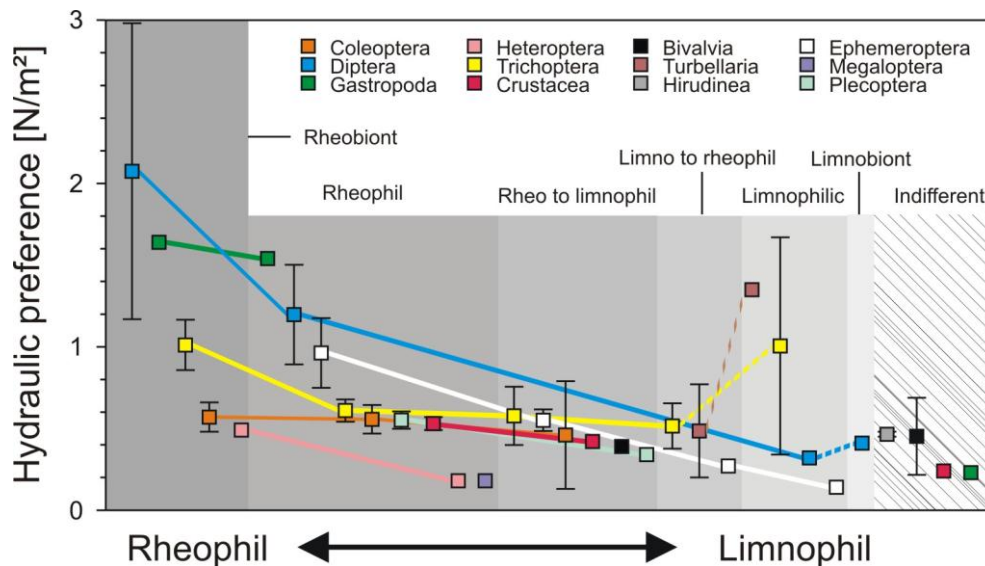


Figure 5 Hydraulic and flow preferences of pooled benthic invertebrates. Colours refer to taxonomic units showing the broad gradients covered.

As already illustrated in the tables of critical flows or shear forces, it is highly important to recognize that the threshold values determined significantly vary between species

within the same genus or family. Thus, for both impact assessment and restoration planning it seems highly relevant to determine diagnostic taxa to the species level, because the higher taxonomic orders commonly contain species with opposing requirements and thresholds, which does not allow for reliable conclusion at that taxonomic level (e.g. Figure 5).

4.4.1 Active avoidance behaviour

Benthic invertebrates are also able to actively avoid hydraulic stress conditions if they increase slowly and continuously. Statzner (1981) showed that *Potamopyrgus* sp. burrows deeper in the sediment when flow conditions exceed baseline levels. The same avoidance behaviour has been reported for caddisflies (Holomuzki & Biggs 2000, Poole & Stewart 1976). Similarly, Schnauder et al. (2010) observed a drag-minimizing body posture of *Calopteryx splendens* and Coenagrionidae sp. (damselflies) to resist increasing shear velocities. In contrast to gradual increases in flow, abrupt changes in hydraulic conditions are thought to outrank continuous intensifications in flow velocity, discharge or shear stress (Imbert & Perry 2000). However, this was not generally supported by a comparative study of critical shear stress thresholds for *Bithynia tentaculata* and *Calopteryx splendens* under continuous flow increases (Schnauder et al. 2010) and abrupt wave pulses (Gabel et al. 2012) in the same sand habitat. Based on this comparison of the two species and a detailed description of invertebrate behaviour during drift tests by Schnauder et al. (2010), it has been concluded that the peak value of shear stress is the main driver of dislodgement for taxa that are not able to powerfully clamp to the sediment, such as gastropods. Other than clamping, individuals of *C. splendens* resisted continuous shear stress increases up to 2.40 N/m² by adopting a drag-minimizing body posture (Schnauder et al. 2010). In contrast, these specimens became washed away by wave-induced shear forces of only 0.13 N/m² (Gabel et al. 2012). This suggests that more mobile and agile species are better able to adapt to continuous flow increases by behavioural changes than rather inflexible species such as gastropods. However, Schnauder et al. (2010) also noted that the common mud snail *Viviparus viviparus* can quickly produce mucus (a behaviour they did not observe for *B. tentaculata*) serving as adhesive anchorage and significantly increased its ability to resist shear stress. It was further observed that the remaining mucus threads prevented the snails from being drifted away even after detachment suggesting that gastropod species might possess species specific resistance behaviour as well (Schnauder et al. 2010).

4.4.2 Flow refuges

Flow refuges are important habitats for benthic invertebrates as they provide shelter from exposure to harsh adverse hydraulic stress conditions (Rempel et al. 1999, Winterbottom et al. 1997). Refuges provide stable substrate structures and low hydraulic stress condition in times of increased discharge that have been shown to severely impact benthic invertebrate communities (Lancaster & Hildrew 1993). Milner & Gilvear (2012) observed step-pool reaches providing more flow refuges for benthic invertebrates during high flow events compared to bedrock, plane-bed, or pool-riffle reaches. Hydraulic dead zones are highly important to maintain diversity and co-existence of benthic invertebrates with varying flow preferences at the mesoscale. By studying the drift responses of five benthic invertebrate species to ship waves in five different habitats, Gabel et al.

(2012) could show that the number of detached individuals decreased with increasing fractal dimension of the habitat (from sand to roots). Therefore, the structural complexity of the habitat where individuals are located in the moment of dislodgement can mitigate the adverse effects of hydraulic forces.

Hydraulic dead zones further enable the accumulation of organic matter and provide food resource patches for detritivorous species even in fast flowing environments. Such resources might be especially important for the establishment of detritivorous species with high dissolved oxygen demands. Regrettably, it is difficult to distinguish if a species' presence is driven by its hydraulic preference or its oxygen demand, as both variables are strongly inter-linked.

To identify species whose presence is not primarily determined by substrate reference or hydraulic preference, preferred substrate classes from 0 (128-256 mm) to 11 (0.125-0.05 mm) according to Singh et al. (2010) were plotted against shear stress (Figure 6).

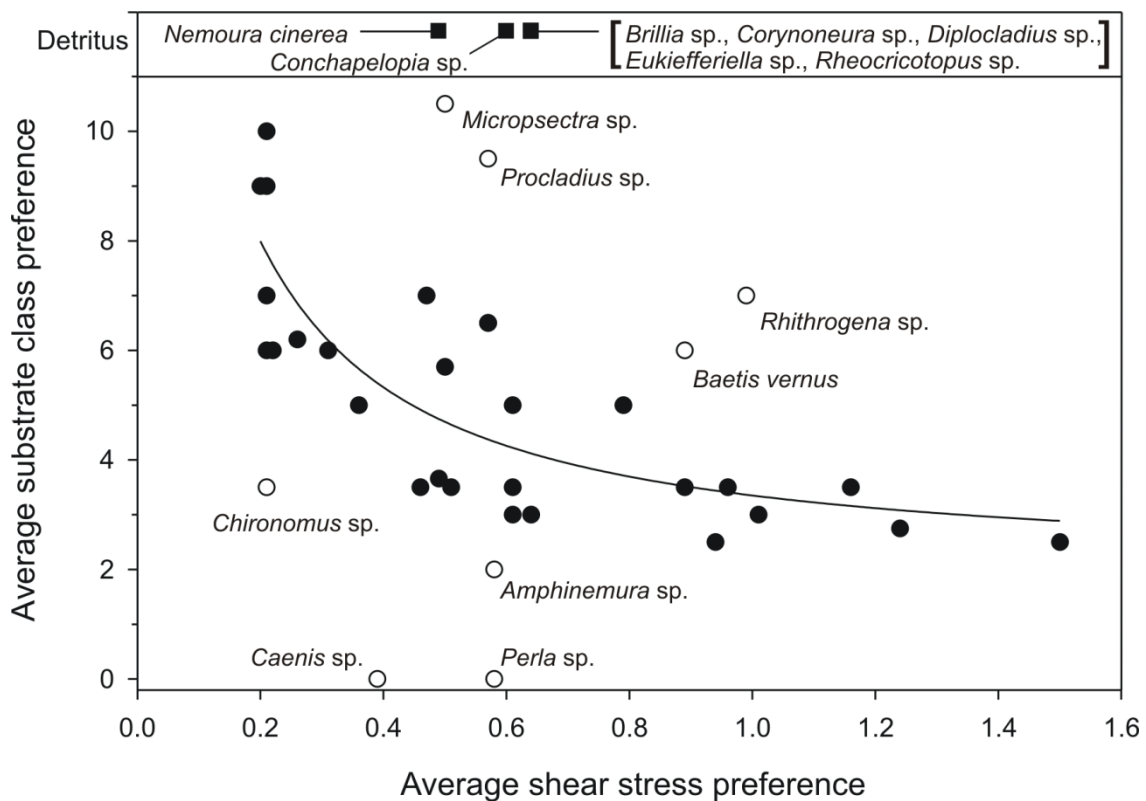


Figure 6 Regression model of substrate preferences of benthic invertebrates from class 0 (128-256 mm) to 11 (0.125-0.05 mm) plotted against their hydraulic preferences. Outliers (white dots) indicate taxa not primarily determined by hydromorphology.

Before plotting substrate class preferences have been averaged over all seasons and most species pooled to the level of genus, Diptera to the level of subfamily to obtain a representative sample size. For species and genera with more than one hydraulic preference reported (compare Figure 5, Table 9), mean values have been used as well. An exponentially decaying regression model provided the best fit (Figure 6). The data have been log-log-transformed and a stepwise outlier analysis according to Fox (1991) per-

formed to identify species and genera whose occurrence is most probably determined by variables other than hydraulic forces and substrate.

The four outliers above the estimated exponential relationship (Figure 6) are well documented as genera having extremely high dissolved oxygen requirements: *Micropsectra* as an oxy-stressor (Brodersen et al. 2008) is sensitive to eutrophication (Johnson 1995) and hypoxic conditions (Quinlan & Smol 2001), *Procladius* is impacted by decreasing oxygen content of the water (Bérg et al. 1962), and the two mayflies *Baetis vernus* and *Rhithrogena* sp. are typical species of running, oxygen rich waters and both very sensitive to oxygen content and velocity (Ambühl 1960). In *Baetis* sp. low dissolved oxygen concentrations were shown to alter microhabitat positioning behaviour, to reduce grazing intensity, and to decrease survival (Lowell & Culp 1999). Of all mayfly species investigated by Ambühl (1960), *Rhithrogena* sp. was reported being most sensitive to decreasing oxygen concentrations. The high oxygen demand of all four species supports the hypothesis that their presence is primarily driven by oxygen saturation rather than grain size (Figure 6). However, all four species prefer finer substrate than commonly provided at the preferred shear force level which indicates a trade-off between food resources and oxygen demand. Thus, these species seemingly depend on moderately flushed, well oxygenated interstitial space providing shelter from flows and sufficient patches of trapped fine organic matter as food resource.

The outliers below the estimated substrate-shear stress relationship are in particular characterized by significantly lower shear force tolerance compared to substrate calibre (Figure 6). *Amphinemura* sp. and *Perla* sp. graze on biofilm respectively predate on other invertebrates (Graf et al. 2002, 2007, 2009) at the bottom side of coarse gravel and substrates where they are exposed to low shear stress levels. *Chironomus* sp. is ubiquitous distributed in slow flowing and stagnant water bodies corresponding to the low shear stress preference. It is further an indicator for eutrophication well capable to tolerate oxygen stress (Bérg et al. 1962) and even able to actively regulate and maintain a constant respiration under decreasing DO conditions (Brodersen et al. 2008). Its appearance in the graph at substrate classes of 16-32 mm has no diagnostic value.

Caenis sp. typically occurs on finer sandy substrate but also on organic detritus and decayed leaves (Int Panis et al. 1994, Pabst et al. 2008). Especially in slowly to moderately flowing rivers, leaves and detritus accumulate between large stones and boulders and thus, the substrate preference of *Caenis* observed by Singh et al. (2010) may primarily reflect the presence of such food source rather than substrate size preference.

4.5 Instream hydromorphological requirements

Beside physical and hydraulic habitat requirements, the distribution of benthic invertebrates within river ecosystems is always related to the regional species pool (Lawton 2000). Thus, an invertebrate species must not necessarily be present at a certain river reach even though the hydromorphological instream requirements are fulfilled (Harrison et al. 2004, Kail & Hering 2005). Nevertheless, some general hydromorphological requirements have been reported that massively positively affect the natural benthic invertebrate fauna.

One key feature of an adequate hydromorphological environment is the provision of a diverse mosaic landscape offering a wide range of complexity (Garcia et al. 2012). There-

fore, the re-development of habitat complexity is addressed by various restoration approaches (Ward & Tockner 2001). Enhancing physical and hydraulic habitat complexity and heterogeneity (the latter often results from the former) by river restoration is commonly sought to improve in-stream biodiversity (e.g. Milner & Gilvear 2012, but see Palmer et al. 2010). However, the direct improvements of benthic invertebrates after rehabilitating habitat complexity have been rather infrequently quantified. By reviewing 18 studies evaluating 78 independent restoration projects Palmer et al. (2010) identified only two which resulted in an increase of benthic invertebrates' diversity (Edwards et al. 1984, Gerhard & Reich 2000, Jungwirth et al. 1993). This dramatic non-effectiveness of restoration projects was explained by a pure focus on improving habitat structure as the primary factor controlling species diversity, thereby neglecting interactions with other (maybe more important) environmental factors such as disturbance, food resources or the regional species pools (Lake 2000, McCabe & Gotelli 2000, Menninger & Palmer 2006, Muotka & Syrjänen 2007, Ward & Tockner 2001, Warfe et al. 2008). Nevertheless, the authors concluded that habitat complexity and heterogeneity could be important factors for invertebrate diversity when other limitations are disposed (Palmer et al. 2010).

The hydraulic habitat heterogeneity in lotic ecosystems is closely related to patterns of benthic invertebrate drift (Hauer et al. 2012) and thus, facilitates the spreading and dispersal of individuals and species. As outlined by Hauer et al. (2012), the continuum of benthic invertebrate drift is often interrupted by pronounced deposition zones, especially in the backwaters of transverse structures such as dams or weirs (see also Boon 1988). The authors analysed critical shear forces and suggested a critical bottom shear stress threshold of 0.25 N/m^2 to maintain the continuum of benthic drift (Hauer et al. 2012). Lower bottom shear forces will support eurytopic or limnophilic species like *Chironomus* sp. or Tubificidae (Hauer et al. 2012), which definitely impacts the ecological status assessment of river water bodies.

Abandoned channels and riparian wetlands that are not permanently connected to the main river channel may suffer from interrupted species drift too (Pan et al. 2012). Therefore, hydrological connectivity with the main channel needs to be maintained to enable constant species turnover and high benthic invertebrate diversity. Pan et al. (2012) proposed that abandoned sections need to be connected, e.g. by flooding, at least once within three years when other anthropogenic impacts are low, otherwise more frequently, e.g. once every year.

4.6 Conclusions

Physical and hydraulic habitat heterogeneity is the main structuring factor for benthic invertebrate communities, but other environmental triggers such as disturbances causing drift events, oxygen demands or the presence/absence of food resources might become controlling factors too.

This meta-analysis especially aimed to identify those species or taxa which sensitively respond to hydromorphological variables and processes and thus, might become diagnostic indicators for hydromorphological integrity as well as pressures and impacts on hydromorphology.

Besides identifying a group of potential indicator taxa showing reliable preferences for coarser bed material and higher shear forces, more general thresholds have been derived

of tolerable flow velocities and shear forces setting physical boundary conditions for habitat suitability and are thus, relevant in restoration planning.

5 Effects of hydromorphology on fishes

Fishes are comparably long-living, mobile organisms with various habitat requirements, habitat shifts during ontogeny, and functional differences between age groups. Thus, fish provide a well suited environmental indicator integrating over large spatial and temporal scales (e.g. Karr 1981, Fausch et al. 1990, Dußling et al. 2004, De Leeuw et al. 2007, Schmutz et al. 2007). This integration over space and time, however, causes major variation in local habitat utilization and accordingly in environmental assessments at the reach scale, where most of the river rehabilitation works are applied (e.g. Roni et al. 2002, 2005, 2008, Kail et al. 2007, Palmer et al. 2010, Feld et al. 2011).

Hydromorphological changes or impacts may set physical thresholds for habitat maintenance or utilisation by exceeding suitable velocities, stream power or depth. Limiting thresholds are commonly mediated by swimming performance and accordingly, affect especially weaker performing functional species or age groups like juveniles (Wolter & Arlinghaus 2003, 2004, Wolter et al. 2004).

Further on, most fish species are well adapted to stochastic environmental fluctuations and tolerate substantial environmental changes, while specialist species sensitively responding to hydromorphological changes are rather limited (compare Chapter 2). Accordingly, most impacts on hydromorphology result in gradual changes of carrying capacity, juvenile fish recruitment, fish density, biomass or abundance structure rather than disappearance of a species. Therefore, thorough environmental impact assessments or evaluation of rehabilitation success require references and before/after sampling designs which are often not available, in particular at larger spatial scales.

In contrast, efficient river rehabilitation should target the key mechanisms or key bottlenecks for specialist species responding to specific habitat structures. Sensitive species are the first to be lost from a local species pool leading to the conclusion that measures to rehabilitate their stocks will be beneficial for a broader range of species too.

5.1 Gravel spawning

Sediment structure and calibre are strongly interlinked with flow velocity. There is a general relation between the flow velocity and the gravel diameter mediated by stream power, with higher flow velocities able to erode and transport coarser substrate. Thus, sediment transport and sediment size distribution fluctuate with the hydrograph: higher flows support a higher transport rate of coarser material and lower flows support a lower transport rate of finer material. In conclusion, a broad variety of flow velocity patterns within a river stretch supports a mosaic of different substrates, textures, and sediment calibres.

While a certain stream power is needed to sustain coarse, well oxygenated, permeable gravel beds, fish species essentially depending on such substrates for spawning principally provide sensitive, diagnostic indicators for hydromorphological integrity. Gravel spawning is commonly considered as adaptation of fish to faster flowing environmental conditions by protecting eggs and hatchling from becoming washed away. Lithophilic fish bury their eggs in or lay them on coarse gravel and the larvae live benthic in the interstitial space (Balon 1975, 1981). Eggs and larvae of lithophilic fish develop in the gravel layer.

Therefore, species of this ecological guild essentially depend on interstitial flow, permeability and especially oxygen supply in the gravel space for their successful reproduction and population development. Accordingly, lithophilic species have been identified as most sensitive to impacts on sediment structure and hydromorphological alterations and in turn should provide highly diagnostic, specific indicators for hydromorphologic impacts.

However, if coarse substrates are maintained despite human alterations of flow velocity, e.g. by moderate wake wash, fish appeared more tolerant against low flow than unsuitable substrates (Arlinghaus & Wolter 2003).

Therefore, reported information on spawning gravel size preferred by fish have been reviewed and analysed to obtain gravel calibre ranges, sorting, and thresholds used by lithophilic fish and relevant for river restoration, in particular for rehabilitating gravel spawning grounds.

5.1.1 Gravel calibre

In total 61 studies were identified presenting data on minimum and maximum sizes and the size composition of spawning gravel for altogether 29 European lampreys and freshwater fish species (Table 10 in the Appendix). This surprisingly low number of species for which specific gravel size information were found strongly contrasted the number of 91 European species considered lithophilic gravel spawner (EFI+ Consortium at <http://efi-plus.boku.ac.at/>). That means that for more than two thirds of the known native species insufficient information is available on specific spawning habitat requirements relevant for using them as diagnostic indicator of hydromorphologic degradation and river rehabilitation.

Most commonly studied were salmonid fish, especially brown trout *Salmo trutta* and of the non-salmonids nase *Chondrostoma nasus* (Table 10-**Error! Reference source not found.**). North American salmonids have been included only if they are established in Europe too, like brook trout and rainbow trout. The gravel requirements of Pacific salmonids have been reviewed and analysed by Kondolf & Wolman (1993) and Kondolf (2000) and were not further analysed here.

Prior to analyses, species were grouped into open substrate spawners (OSP) and brood hidiers (BH) according to Balon (1975, 1981). This differentiation seemed highly relevant, because the latter dig redds up to >40 cm deep (e.g. reviewed by Chapman 1988) in the gravel, which has two ecological implications: i) BH require deep, permeable, well oxygenated gravel layers and ii) the usable gravel calibre is limited to a maximum size which can be moved by the specimen digging the red. In contrast, OSP should be able to use clean surfaces of even larger gravel calibres for spawning and further tolerate less permeability and higher contents of fine sediment in deeper gravel layers (>5 cm).

Missing data have been completed as much as possible; however, in particular the gravel metrics could not be converted if either means or min-max values were reported. If not indicated in the source, average fish lengths have been taken from FishBase (Froese & Pauly 2013). Differences and variations in gravel usage by guilds and species of lithophilic fish have been analysed using all data sets of the rarely studied species and random selection of a corresponding number of data sets (2-3) of the frequently studied species.

As expected, OSP used much broader variety of gravel calibres and especially gravel of substantially larger gravel diameter (Figure 7). However, within both groups no significant trends or correlation with fish length were found.

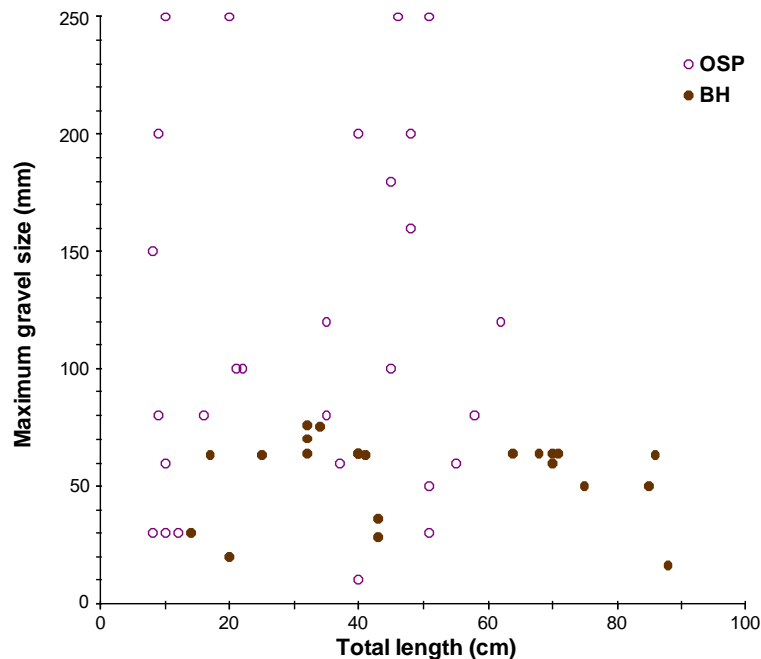


Figure 7 Scatter plot of fish length related to the maximum usable spawning gravel size reported for lithophilic brood hider (BH) and open substrate spawner (OSP).

In contrast, the differences between both spawning types were highly significant (Table 4, Figure 9). Although average OSP were significantly smaller, they used significantly larger pebbles, with an upper mean of 118 mm diameter compared to 55 mm for brood hider (Table 4).

Even if not apparent in the data compiled (compare Table 10-Table 13, Figure 7), significant empirical relations between fish length and gravel diameter have been reported for red digging salmonids (Kondolf & Wolman 1993, Crisp 1996), compare Figure 8.

While integrating over three species – brown trout, Atlantic salmon *Salmo salar*, and grayling *Thymallus thymallus* – Crisp (1996) reported the empirical relation of median grain size of gravel (P mm): $P = 0.5 L + 4.6$, with L = fish length (cm). Kondolf & Wolman (1993) have discussed the difference between ability and choice of a specimen; while large females are able to lift more weight and hold in stronger currents, they might choose smaller gravels in less gradient reaches. Therefore, the authors came up with an envelope curve that fish can use gravels with median diameter up to 10% of their body length (Kondolf & Wolman 1993) (Figure 8).

Table 4 Comparisons between lithophilic brood hidere (BH) and open substrate spawners (OSP) of spawning gravel used, spawning depth, flow velocity, spawner length, and species' FRI compiled from literature sources (N= sample size, SD= standard deviation, SE=standard error).

Variable	Spawning type	N	Mean	SD	SE	t-value	df	Significance p=
Minimum gravel size (mm)	BH	23	8.06	6.331	1.320	-2.617	41	0.012
	OSP	30	16.02	15.000	2.739			
Maximum gravel size (mm)	BH	23	55.43	17.191	3.585	-4.183	30	0.000
	OSP	28	118.21	77.127	14.576			
Mean gravel size (mm)	BH	8	37.58	32.993	11.665	-0.722	11	0.486
	OSP	8	47.08	17.186	6.076			
Total length (cm)	BH	26	48.65	22.956	4.502	2.919	54	0.005
	OSP	30	32.73	17.811	3.252			
Minimum depth (m)	BH	20	0.18	0.084	0.019	-0.806	16	0.432
	OSP	15	0.23	0.248	0.064			
Maximum depth (m)	BH	20	0.62	0.229	0.051	-1.341	17	0.198
	OSP	16	0.93	0.896	0.224			
Mean depth (m)	BH	14	0.33	0.116	0.031	-0.350	16	0.731
	OSP	4	0.35	0.123	0.062			
Minimum flow velocity (m/s)	BH	23	0.24	0.211	0.044	-0.868	41	0.391
	OSP	20	0.30	0.219	0.049			
Maximum flow velocity (m/s)	BH	22	0.68	0.353	0.075	1.198	42	0.238
	OSP	22	0.57	0.237	0.051			
Mean flow velocity (m/s)	BH	11	0.40	0.116	0.035	-1.477	12	0.165
	OSP	3	0.51	0.146	0.085			
Fish Region Index (FRI)	BH	26	4.68	0.728	0.143	-6.960	53	0.000
	OSP	29	6.07	0.752	0.140			

No significantly different requirements exist in regard to flow velocities and depth at the spawning sites (Table 4), which seems plausible, due to the depth and velocity related stream power and sediment transport processes maintaining the spawning sites (e.g. Hauer et al. 2011).

Most interesting and relevant for river rehabilitation are especially two findings: Firstly, both spawner types overlap in mean gravel size and do not significantly differ in mean gravel diameter. This finding implicates that a range in gravel calibre between about 4 mm and 69 mm (corresponding to BH mean \pm SD) should fit for all lithophilic fish and rehabilitation of gravel bars for spawning focus on similar calibres. Correspondingly, in a spawning habitat rehabilitation project for brown trout and Atlantic salmon the addition of gravel dominated by 64-124 mm size classes was observed too coarse for spawning (Barlaup et al. 2008).

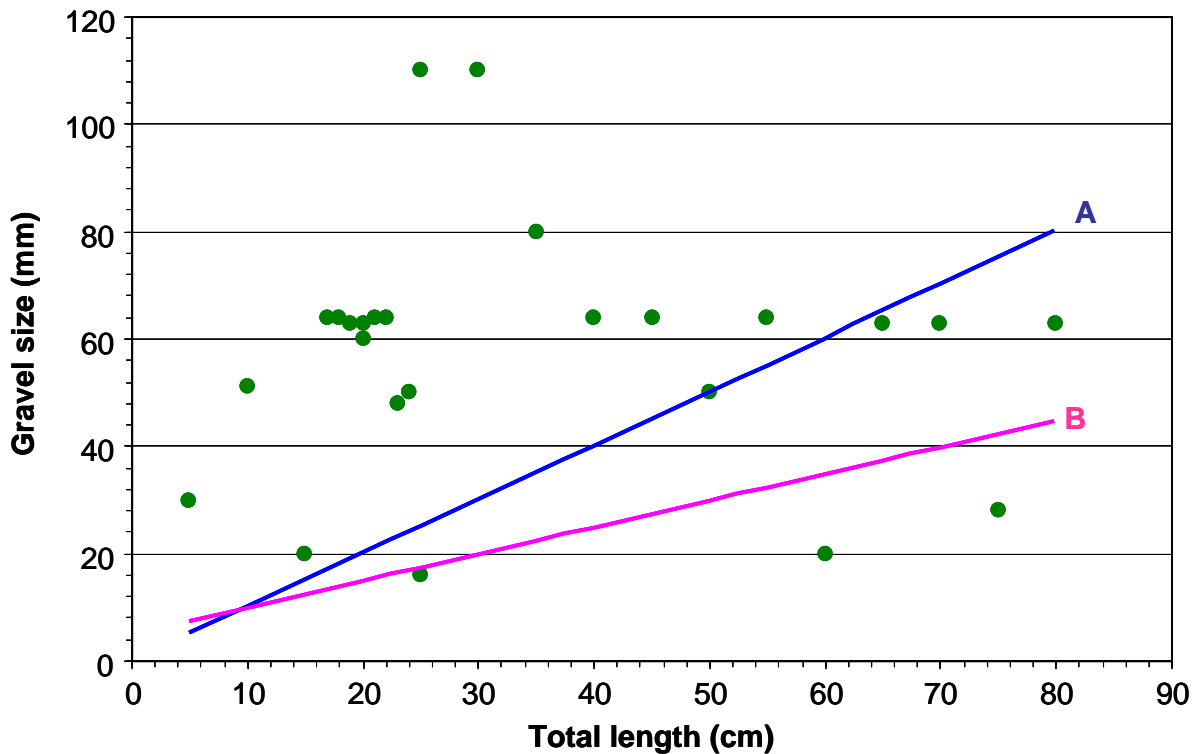


Figure 8 Empirical relation between female spawner length and median spawning gravel calibre in brood hiding salmonids after A) Kondolf/Wolman 1993) and B) Crisp 1996); green dots = maximum values reported.

Secondly, both spawner types significantly differ in their average Fish Region Index (FRI). This metric is a river zonation qualifier for a species and gives its weighted probability to occur in a certain river region under natural conditions (Schmutz et al. 2000, Dußling et al. 2004, 2005). It will be introduced in more detail later on. According to their mean FRI brood hidiers are commonly more upstream distributed in the headwaters (trout to barbel region) compared to OSP mainly in the lowland bream region (Figure 9). Accordingly, in lower river sections and lowland rivers rehabilitation might focus more on the gravel surface than on deeper layers and might further use larger gravel. The latter might become especially important if other needs beside gravel provision have to be met at the same time, e.g. flood protection or bank protection in navigable waters (e.g. Söhngen et al. 2008). For example regulation structures in waterways like groynes and parallel dikes could to a certain degree substitute natural spawning sites if the heads respectively main channel sides are constructed using suitable gravel sizes (Bischoff & Wolter 2001, Niles & Hartman 2009).

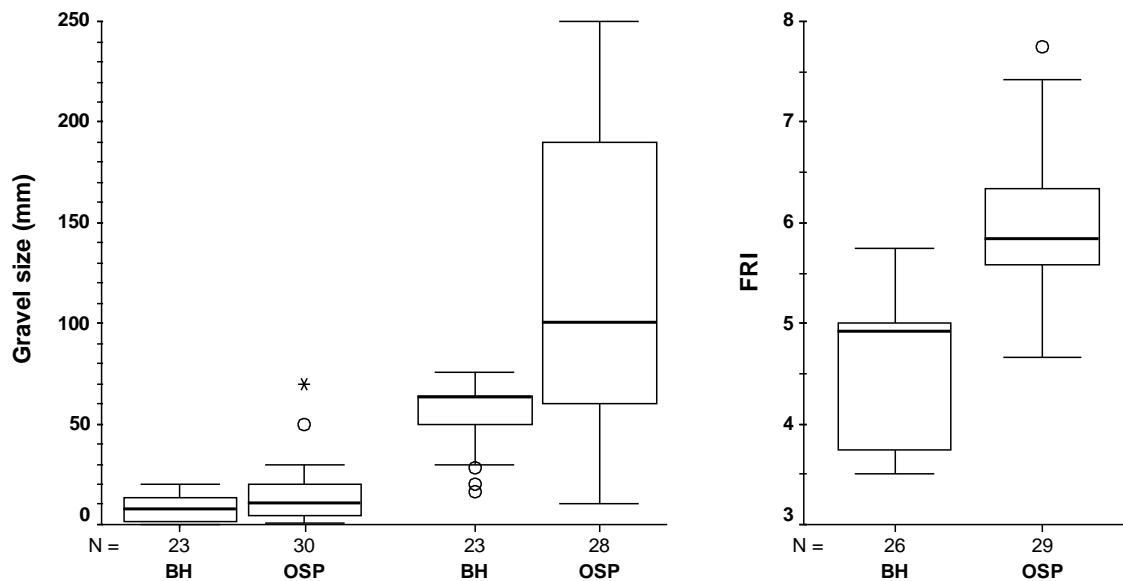


Figure 9 Boxplots of left: minimum and maximum gravel size reported and of right: species-specific Fish Region Indices (FRI) paired between brood hidiers (BH) and open substrate spawners (OSP); indicated are 25th and 75th (boxes) 10th and 90th (whiskers), median and outliers.

5.1.2 Gravel permeability and effects of fine sediment loads

Brood hidiers do not only require a certain gravel calibre, but also a certain depth layer of permeable sediment with interstitial flow of oxygen rich water. Egg burial depth of various salmonid species have been reviewed by DeVries (1997) and ranges on average between 5 cm and 30 cm below the bed level with reported maxima up to 51 cm in coho salmon (Burner 1951, cited in DeVries 1997). However, for brown trout Sternecker et al. (2013) reported a negative correlation between egg burial depth and hatching success of the eggs, with an observed decline by 26% from 50 mm to 150 mm sediment depth. Correspondingly, Riedl & Peter (2013) reported a very low average egg burial depth of 3.8 cm below original bed level for brown trout from Alpine rivers, although they should be principally exposed to higher stream power and scour there.

The interstitial water quality was identified as a limiting factor for salmonid egg development (e.g. Sternecker et al. 2013). The availability of oxygen to incubating salmonid embryos depends on the exchange of channel water with the gravel riverbed. The hydromorphologic processes driving this exchange include bed permeability and surface roughness effects, while the flux of oxygenated water through riverbed gravels is controlled by gravel permeability, coupling of surface-subsurface flow and oxygen demands imposed by materials infiltrating riverbed gravels (Greig et al. 2007). Chapman (1988) has calculated gravel permeability between 10,000 cm/h and 13,000 cm/h (values taken from Figure) for 50% survival to emergence of chinook *Oncorhynchus tshawytscha* and coho salmon *O. kisutch*, respectively, which corresponds to interstitial flow velocities of 0.028-0.036 m/s. Lotspeich & Everest (1981) suggested a new measure of the quality of riffle gravels for salmonid reproduction: the fredle index (fi). This index is a ratio of the geometric mean grain size and the gravel sorting coefficient both proportional to pore size and permeability. Both variables regulate intragravel water velocity and oxygen

transport to incubating salmonid embryos and control intragravel movement of alevins (Lotspeich & Everest 1981). A value $f_i = 5.0$ was determined as permeability threshold where the survival to emergence exceeded 90% for both chinook and coho salmon (Chapman 1988). The Fredle index has been shown to higher correlate with survival than the geometric mean grain size, but the calculation of the index requires additional sediment size and sorting data often not available from standard surveys (Jensen et al. 2009).

The proportion of fine sediments is inversely correlated to permeability and Fredle index and therefore, detrimental to the survival of eggs and embryos in the interstitial. Harrison (1923) was one of the first to report an inverse relationship between the quantity of sand and silt in redds and the survival of incubating salmonid eggs. Accumulation of fine sediments at gravel spawning sites constitute a major hydromorphological impact on lithophilic fish as well as on gravel preferring invertebrates as illustrated in Chapter 4. However, the fine sediment input is a somewhat diffuse concept because various authors had very different perceptions of "fine" particle size ranging from clay <0.004 mm (Greig et al. 2005), silt <0.063 mm (Lapointe et al. 2004), and fines <0.85 mm (Chapman 1988, Jensen et al. 2009) to sands <2 mm (Lapointe et al. 2004, Riedl & Peter 2013), <4.75 mm (Platts et al. 1989), <6.4 mm (Reiser & Bjornn 1997, Tappel & Bjornn 1983, Jensen et al. 2009), up to 5-8 mm (Sterneckner & Geist 2010) and 9.5 mm (Tappel & Bjornn 1983).

From the available studies – mostly on Pacific salmon (e.g. McNeil & Ahnell 1964, Lotspeich & Everest 1981, Tappel & Bjornn 1983, Chapman 1988, Geist et al. 2002, Jensen et al. 2009) but also on Atlantic salmon (Soulsby et al. 2001, Julien & Bergeron 2006, Heywood & Walling 2007) and trout (Soulsby et al. 2001) – the ecologically most relevant fraction of fines appeared <1 mm. Accumulation of fines <1 mm has been reported causing most significant impacts on hatch and survival of fish larvae even at rather low proportions.

In Pacific salmon odds of egg-to-fry survival dropped between 13% and 18% with the increase of fines <0.85 mm by 1% and the survival rapidly declined if the proportion of fines <0.85 mm increased 10% (Jensen et al. 2009). This steep decrease in survival was levelling out at <10% when the proportion of fines was >25% (Jensen et al. 2009). Correspondingly, Julien & Bergeron (2006) observed 71% survival of Atlantic salmon fry at 10.3% fines <1 mm in contrast to 11% survival at 27.2% fines. The latter value was also nearly equal the lethal limit for fine sediments <2 mm of 25% by volume established by Reiser & Bjornn (1979). However, Heywood & Walling (2007) reported the survival of Atlantic salmon embryos falling below 50% when sediment <1 mm composed more than about 8% of the redd and reaching zero at around 12% sediment <1 mm.

In contrast, in a lab experiment Fudge et al. (2008) observed altered emergence patterns in rainbow trout at the highest level of 28.6% mixed fines (11.2% <2 mm and 17.4% 2-4 mm), but no significant differences in overall emergence being above 70% in all treatments.

It should be further considered, that especially the brood hidens also actively clean the sediments while digging their redds. For example, McNeil & Ahnell (1964) found that pink salmon significantly reduced the percentage of solids in the substrate that passed through sieve openings of 0.833 and 0.104 mm, and that a portion of the removed materials consisted of light organic material. New redds can contain as much as 32% less or-

ganic material than old redds constructed in the previous year (Ringler 1970, cited by Chapman 1988).

In conclusion, accumulation of fine sediments <1 mm grain size during the incubation period pose a significant threat to brood hiding gravel spawners and impact on embryo survival at levels of about 10% in the substrate's surface layer.

This impact becomes further pronounced by the sedimentation of silt and organic material. In lab incubation experiments using Atlantic salmon eggs at sand contents of about 10%, the addition of 1% silt had a more than three times higher detrimental effect on survival than a 1% increment in sand (Lapointe et al. 2004).

In a two years field experiment performed by Levasseur et al. (2006), the proportion of silt <0.125 mm in the redds explained 83% of the variation in Atlantic salmon embryo survival, with a threshold at approximately 0.2%, above which survival dropped sharply below 50%. At rather comparable contents of fines <2 mm between 10% and 15.7%, the survival of Atlantic salmon eggs dropped from 71% to 28% and 8.7% at contents of organic matter of 3.4%, 7.5% and 19.7%, respectively (Greig et al. 2005).

Rehabilitation measures addressing the provision of gravel bars and spawning gravel should not only use rounded material in a size range of 4-69 mm, but also limit the supply of fine sediments <1 mm below about 10% and organic material below 5%, e.g. by establishing a sufficient flow velocity washing out the fines.

5.2 Flow velocity and swimming performance

Aquatic organisms are exposed to flow velocity and stream power, which both not only provide and maintain riverine habitats and structures, but also set physical thresholds for its utilisation. Abilities and limitations to withstand flow velocities and shear stress have been described for plants and invertebrates, and they exist for fish as well (e.g. Floyd et al. 1984, Schlosser 1985, Copp 1992, Zauner & Schiemer 1992, Copp & Garner 1995, Scheidegger & Bain 1995, Garner 1999, Jackson et al. 2001, Arlinghaus et al. 2002, Schwartz & Herricks 2008, Kucera-Hirzinger et al. 2009, Huckstorf et al. 2011).

Swimming performance of fish has been reviewed and analysed as proxy to determine their ability to withstand absolute physical forces set by flow velocity (Wolter & Arlinghaus 2003, 2004). Knowledge of fishes' swimming performance is prerequisite to assess impacts from inland navigation or hydro-peaking on fish and further serves in designing proper migration facilities for fish.

Among others, in particular spawning migrations, habitat shifts, dispersal and habitat maintenance in hydro-dynamically determined environments are of profound ecological importance and depend substantially on the individuals' capacity for locomotion (e.g. Kolok 1999, Plaut 2001). With regard to hydrodynamics, absolute swimming performance was considered as ecologically most relevant, because the hydrodynamic characters of the habitat represent physical thresholds determining minimum swimming requirements for habitat use to avoid displacement (Wolter & Arlinghaus 2003, 2004).

The swimming performance of fish is characterized by the relation of swimming speed and time until fatigue. According to the endurance time it has been classified into sustained, prolonged, critical, and burst swimming maintained for >200 min, >60-200 min, ≤60 min and ≤20 s, respectively (Brett 1964, Webb 1975, Beamish 1978). The individual

swimming performance depends on species, swimming mode, size, temperature, ontogenetic stage, photoperiod, oxygen tension, pH, salinity, and various pollutants and toxins, with total length as paramount trait (reviewed in Randall & Brauner 1991, Videler 1993, Hammer 1995, Domenici 2001, Wolter & Arlinghaus 2003).

The literature had been reviewed for studies on fish swimming performance and a total of 168 identified which provided results for altogether 75 freshwater fish species exercised under comparable conditions (for details see Wolter & Arlinghaus 2003). These data were used to compute burst and critical swimming performance for freshwater fish of various ecological guilds as function of total length (Wolter & Arlinghaus 2003, 2004). A power model fitted best.

Burst swimming performance (U_{burst}) was modelled for specimen up to 60 mm total length (Figure 10). The general models of length-specific burst and critical swimming performance were highly significant. As expected, salmonids exhibited the highest burst swimming performance; however, the differences detected between the small-sized individuals of different taxonomic orders were not significant (F-test, $p = 0.142$). Thus, the threshold of swimming performance shown in Figure 10 applies for all fish up to 60 mm total length, which is important as one would intuitively think that rheophilic fish perform superior to eurytopic and limnophilic fish. Consequently, a 56 mm long fish already maintains a speed of 1.0 m/s for 20 s, but only 0.54 m/s in the critical mode for one hour (Figure 10).

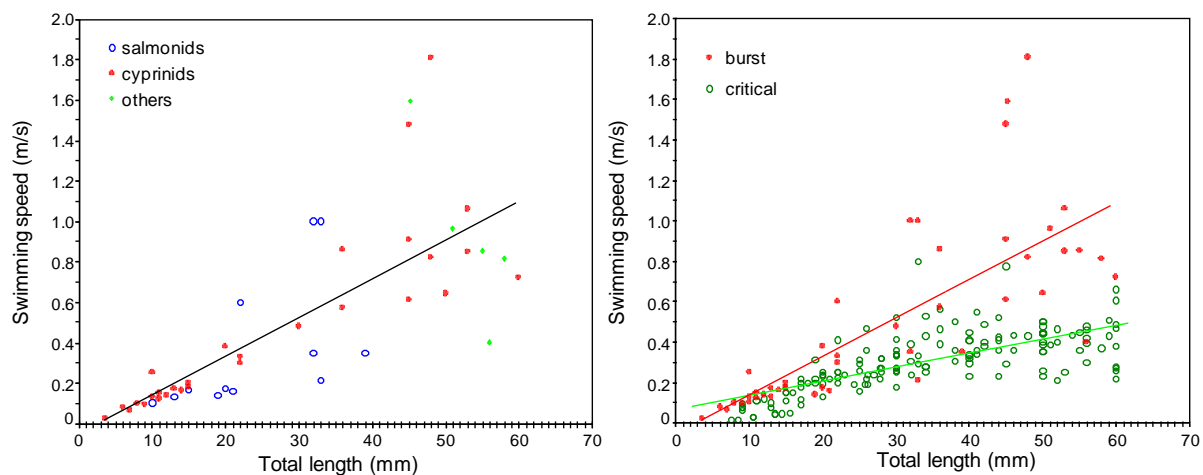


Figure 10 Burst swimming performance (left) of salmonids, cyprinids and other fish species up to 60 mm total length compared to their critical swimming performance (right). Regressions did not significantly differ between families (F-test, $p = 0.142$) and followed the models $U_{burst} = 0.0068 TL^{1.24}$ ($df = 84$, $R^2 = 0.83$; $p < 0.001$) and $U_{crit} = 0.0067 TL^{1.09}$, ($df = 155$, $R^2 = 0.60$, $p < 0.001$); modified from Wolter & Arlinghaus (2003).

Due to the performance generally sinking with duration, even larger fish might become affected by a longer lasting or permanent exposure to higher flows. Therefore, the critical swimming performance has been modelled for specimens up to 20 cm total length (Wolter & Arlinghaus 2004).

The general model obtained for all species was $U_{crit} = 0.0158 TL^{0.80}$ ($df = 239$, $R^2 = 0.65$, $p < 0.001$). According to this model a fish of 17.9 cm total length performs a critical

swimming speed of 1 m/s. However, in this length range the critical swimming performance significantly differed between families. Surprisingly, the critical performance of rheophilic cyprinids significantly exceeded those of salmonids as generalist swimmers, with a 13.3 cm long cyprinid swimming as fast as a 20.1 cm long salmonid.

The following taxa-specific models have been obtained for the critical swimming speed (Wolter & Arlinghaus 2004): i) salmonids $U_{crit} = 0.0198 TL^{0.74}$ (df= 49, $R^2 = 0.71$, $p < 0.001$), ii) cyprinids $U_{crit} = 0.0165 TL^{0.84}$ (df= 111, $R^2 = 0.76$, $p < 0.001$) and iii) other species $U_{crit} = 0.0654 TL^{0.42}$ (df= 50, $R^2 = 0.33$, $p < 0.001$).

Freshwater fish larvae hatch at total length of 2.7-9.5 mm and swim free with 6-15 mm. In this stage their burst performance range is about 0.06-0.20 m/s and their critical swimming speed about 0.05-0.13 m/s. Therefore, larvae and juveniles of freshwater fish essentially depend on the availability of shallow, low flowing shore line refuges for feeding and shelter and with them the successful natural recruitment of most of the freshwater fishes. In contrast older and larger fish become hardly limited by flow velocities, except for flush flows and hydro-peaking. In particular structured river beds as well as substrate roughness significantly reduce flow velocities and provide shelter even for relatively small bodied fish. Therefore, river rehabilitation has to consider especially the provision of wake wash protected, low flowing, shallow littoral habitats for juvenile fish recruitment as common bottleneck in regulated manifold used river systems (e.g. Wolter et al. 2004).

5.3 Habitat complexity and fish

As pointed out above, gravel spawning is commonly considered as adaptation of fish to fast flowing environmental conditions by protecting eggs and hatchlings from becoming washed away. However, average cross-section flow velocities and preferred flow velocities at spawning sites of riverine fishes of 0.2-1.0 m/s (e.g. Mann 1996, Riedl & Peter 2013) are well above the swimming ability of emerging fry even in lowland rivers (see above). Fish larvae emerge from the spawning substrate to the water column when the yolk sac exhaustion is almost complete (Bardonnnet 2001). During emergence the larvae become exposed to the flow and because of their low swimming abilities early larvae become easily entrained and transported by flow, leading to downstream displacement. Therefore it was hypothesized, that in rivers the initial distribution of emerging fish larvae is accidentally, related to hydrodynamic forces, structural complexity, and trapping structures (Pearsons et al. 1992, Schiemer et al. 2001, Wolter & Sukhodolov 2008).

Drift studies provided empirical evidence for such a hypothesis. For example, small centrarchids and cyprinids <10 mm were found extremely susceptible to downstream displacement by flows (Harvey 1987). Temporal peaks in drift patterns have been observed early in the season when most larvae emerge, e.g. in the lower River Elbe (Oesmann 2003), in the Czech lowland rivers Morava and Kyjovka (Reichard et al. 2002) and in the Austrian Danube River (Zitek et al. 2004). Generally, the passive downstream drift of fish larvae by current without orientation to it was considered as the most common mode of spatial displacement (Pavlov 1994) and the timing of fish in the drift apparently a function of spawning time (Brown & Armstrong 1985, Reichard et al. 2002, Zitek et al. 2004).

The heterogeneity of the flow structure, particularly the presence of low-transit zones and backwaters, controls the downstream displacement of fish and determines the avail-

ability of shelter and nursing habitats (Sukhodolov et al. 2009). As a result, a complex mosaic of flow-protected habitats, gravel bars, large wood deposits, diverse sediment structures, and scour pools, is pivotal for maintaining diverse, self-recruiting, and native fish assemblages in rivers (Pearsons et al. 1992, Jungwirth et al. 2000, Bardonnnet 2001, Schiemer et al. 2003, Armstrong & Nislow 2006).

By developing and validating a model of dispersion processes with non-transit zones, Wolter & Sukhodolov (2008) studied the effect of flow, channel geometry, and retention zones on the distribution of juvenile fish. The retention of fish was highly significantly related to the availability of recirculation currents, non-transit zones, and shelter which all directly refers to bank line complexity and habitat heterogeneity. The number of fish retained in the dead zones increased an order of magnitude with a three times increase in dead zone volume (Wolter & Sukhodolov 2008). Substantial increase in settled juveniles was also notable with an increase in the dead zones retention time. Both, development and persistence time of dead zones were inversely related to water depth and decreasing vegetation cover (Wolter & Sukhodolov 2008).

In lowland rivers structural complexity and low flowing nurseries for fish larvae and juveniles are in particular provided in the inner bends of meanders and side waters as well by instream structures like dead wood, roots of the riparian vegetation and aquatic plants (e.g. Grenouillet et al. 2000, 2002, 2004, Duncan et al. 2001, Grenouillet & Pont 2001, Sindilariu et al. 2006). In contrast, in lower mountain and higher altitude rivers aquatic vegetation is commonly absent and pools and large stones the most important instream structures providing shelter from flow. Here, multiple channels in braided river sections and forming islands provide recirculation flows and the necessary low flowing shallow refuges for juvenile fish. For stretches of the rivers Tagliamento and Adige (both Italy), Sukhodolov et al. (2009) have modelled the performance for dispersal of fish embryos or larvae of multi-thread, braided reaches compared to single-thread stretches with alternate bars. The model indicated that braided channels provide much more complexity and favourable nurseries and retain ten times more fish embryos and larvae (Sukhodolov et al. 2009). At a distance of 1 km from a potential spawning area, the number of retained embryos and larvae was about 10% in braided compared to <1% in single-thread channels with alternate bars (Figure 11, Sukhodolov et al. 2009). Accordingly, the distance to retain 50% of the fry emerged was six kilometre in the braided reach compared to nearly 70 km in the single-thread reach (Figure 11) corresponding to a ten times higher carrying capacity for juvenile growth of the first, more complex and structured reach.

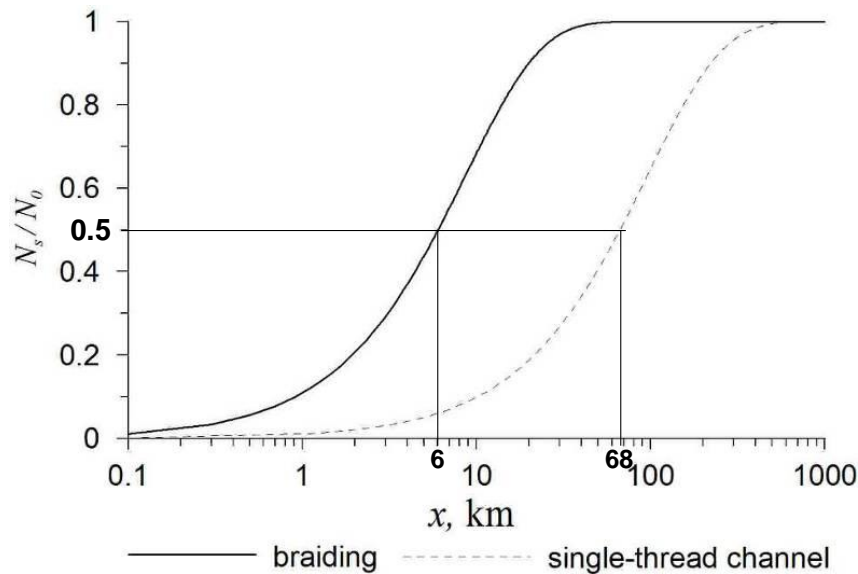


Figure 11 Modelled longitudinal distribution of emerging fish fry from a spawning area in a braided (solid line) compared to a single-thread channel (dashed line). Thin lines indicate the distance required to retain half of the emerged embryos. Modified after Sukhodolov et al. (2009).

Empirical evidence for the positive correlation between habitat complexity and the capacity for juvenile fish recruitment has been further reported from several comparative studies of juvenile fish nurseries and recruitment in unregulated and degraded river stretches (Copp 1990, 1997, Bryan & Scarnecchia 1992, Wolter & Vilcinskas 1997, Jurajda 1999, Berrebi-dit-Thomas et al. 2001, Grift 2001, Jurajda et al. 2001, Pont & Nicolas 2001, Arlinghaus et al. 2002, Sindilariu et al. 2006, ˇiliukas & ˇiliukienė 2009, Huckstorf et al. 2011).

To sum up, the availability of shallow, low flowing habitats maintained by structural complexity of the banks is essential for the recruitment of nearly all fish species in rivers (Harvey 1987, Wolter & Vilcinskas 1997, Schiemer et al. 2003, Strayer & Findlay 2010).

For adult fish a decrease of structural habitat complexity was principally reported detrimental to fish diversity, fish species richness and fish species composition (e.g. Zauner & Schiemer 1992, 1994, Wolter & Vilcinskas 1997, 2000, Penczak & Kruk 2000, Raat 2001, Wolter 2001, 2008, Rhoads et al. 2003, Vasil'eva 2003, Aarts et al. 2004, Weber et al. 2011), while its increase has shown increases as well as decreases or no measurable changes of fish assemblages (Smokorowski & Pratt 2007). The latter has been suggested resulting from a threshold response of fish to environmental changes (e.g. Harding et al. 1998) respectively from insufficient spatial scales of measures and/or temporal scales of evaluations (Smokorowski & Pratt 2007).

In principal the positive response to structural complexity and habitat heterogeneity of adult fishes is similar to juvenile conspecifics, but in contrast to the latter not determined by physical thresholds set by flow velocity and stream power. The adult fish response to habitat complexity reflects a generally positive association with the availability and varie-

ty of resources, food, refuges, and habitats (e.g. Smokorowski & Pratt 2007, Strayer & Findlay 2010). Positive effects of heterogeneous bank structures were still observable in regulated rivers and waterways, where species richness, species diversity and fish density were significantly positively correlated to those, e.g. in German lowland waterways (Wolter 2001) and in the River Danube (Hirzinger et al. 2004). At the global scale habitat heterogeneity and net primary productivity constituted the dominant effects on global fish diversity patterns (e.g. Guégan et al. 1998, Oberdorff et al. 2011).

Especially the large fish use deep pools and large wood accumulations as shelter, feeding place, for hiding, resting, and overwintering (Fette et al. 2007, Schwartz & Herricks 2008). Accordingly, their biomass was positively correlated to pool depth, pool density and the amount of shelter structures, which altogether determined the carrying capacity and standing stock of adult fish (Fette et al. 2007, Schwartz & Herricks 2008). In their meta-analyses of the effects of physical habitat change on fish, mainly salmonids, Smokorowski & Pratt (2007) found a direct link between habitat complexity and fish abundance or biomass, with fish biomass most strongly responding to habitat change. The latter seems consistent with the positive response of large fish to deeper pools and structures observed by Fette et al. (2007) and Schwartz & Herricks (2008). However, at larger spatial scales the results became rather ambiguous regarding the net change in fish assemblages, whether there was an increase in abundance and biomass or just a redistribution of already existing fish (Smokorowski & Pratt 2007).

An alternative approach of linking species distribution patterns with current environmental conditions uses species distributions models (SDMs). Although SDMs are commonly applied to predict future species distribution patterns following climate change projections (e.g. Buisson et al. 2008b, 2013, Markovic et al. 2012 and references cited therein), they similarly relate current conditions to current species distributions and will accordingly also identify significant species' relations to hydromorphological parameters. For example, by modelling distribution patterns of 38 freshwater fish species across Germany the cumulated upstream river length and Strahler order were found of high predictive power and importance (Markovic et al. 2012). Strahler order provides a suitable proxy for the upstream – downstream gradient and river type by integrating over all hydro-physical characters along the river network. Strahler order alone described a large portion of the spatial distribution pattern of barbel *Barbus barbus* in Germany (Markovic et al. 2012). Similarly, the occurrence of French headwater fishes was significantly determined by their specific response to river zones (Pont et al. 2005).

The most important factors in predicting freshwater fish diversity were related to components of river size, like drainage area (Oberdorff et al. 1995, 2011, Joy & Death 2004, Pont et al. 2005), stream order (Penczak & Mann 1990, Joy & Death 2004, Markovic et al. 2012), river slope (Pont et al. 2005), flow regime (Oberdorff et al. 1995, Fleituch & Amirowicz 2005, Snelder & Lamouroux 2010), Froude number (Lamouroux et al. 2002, Lamouroux & Souchon 2002, Fleituch & Amirowicz 2005), or the position in the stream gradient (Buisson et al. 2008a, 2008b, 2013, Grenouillet et al. 2008, Buisson & Grenouillet 2009).

The identified predictors of fish diversity integrate over hydromorphologic characters at larger spatial units reflecting the longitudinal array of functional process zones in rivers (Thorp et al. 2006) and accordingly, also the sequence of biocoenotic river regions with

differentiated species assemblages (Thienemann 1925, 1926, Huet 1949, 1953, Illies 1961, Illies & Botosaneanu 1963). These findings strongly support the concept of species-specific river zonation indices as metric or species' trait which integrates over relevant hydromorphological features.

5.4 River zonation and the Fish Region Index (FRI)

Rivers are longitudinally structured into functional process zones from the krenal to the hypopotamal which become suitable for fish with the epirithral reach. The concept of fish regions is based on the empirical knowledge that these river zones constitute biocoenotic regions with distinct fish communities, referring to as fish regions (Frič 1872, von dem Borne 1882, Thienemann 1925, 1926, Huet 1949, 1953). However, beside the eponymous reference species for each fish region, there was a varying number and composition of accompanying species with most of them typically occurring in more than one fish region.

To overcome these uncertainties the Fish Region Index (FRI) has been developed to characterise all fish species by means of their natural probabilities of occurrence in the river regions relevant for fish: 3 Epirithral (upper trout region), 4 Metarhithral (lower trout region), 5 Hyporhithral (grayling region), 6 Epipotamal (barbel region), 7 Metapotamal (common bream region), and 8 Hypopotamal (ruffe-flounder region). Based on previous indices developed and harmonised for Austria (Schmutz et al. 2000) and Germany (Dußling et al. 2004, 2005), this project has classified a total of 163 European lampreys and fish species according to their expected occurrence in the six different river regions under unimpaired conditions using available fish distribution data and expert judgement (Table 11). Here, special thanks go to the experts who contributed to this species classification without being part of the REFORM consortium: Jost Borcharding (University of Colon), Konrad Gorski (University of Concepcion), Tibor Erös (Balaton Limnological Research Institute of the Hungarian Academy of Sciences), Teresa Ferreira (University of Lisboa), Jörg Freyhof, Jörn Gessner (both IGB), and Gabor Guti (Danube Research Institute).

5.4.1 Calculation of FRI

The longitudinal distribution of a given fish species was described by its expected occurrence in the six different river regions under unimpaired conditions by scoring the species' probability of occurrence for each river region with expectation values from 0 to 12, with the sum of all expectation values equals 12. Based on the resulting weighted distribution and using the probability values for each river region (compare Table 11) the Fish Region Index (FRI) was calculated as weighted averages according to Sachs (1997) (Dußling et al. 2004, 2005):

$$FRI = \frac{3 \cdot p_3 + 4 \cdot p_4 + 5 \cdot p_5 + 6 \cdot p_6 + 7 \cdot p_7 + 8 \cdot p_8}{12}$$

with $p_3 \dots p_8$ = probabilities of occurrence from epirithral (3) to hypopotamal (8) from 0 to 12, in sum 12. FRI values range from 3.00 ($p_3 = 12$) to 8.00 ($p_8 = 12$).

The FRI indicates the average preference of a given fish species for a certain river region and its variance (S^2 FRI) indicates how much the occurrence of a given species spreads over several river regions. This variance was calculated based on the weighted distribution of probabilities as weighted variance according to Sachs (1997) (Dußling et al. 2004, 2005):

$$S^2 \text{ FRI} = \frac{p_3(3-\text{FRI})^2 + p_4(4-\text{FRI})^2 + p_5(5-\text{FRI})^2 + p_6(6-\text{FRI})^2 + p_7(7-\text{FRI})^2 + p_8(8-\text{FRI})^2}{11}$$

The variance increases with the species' natural spread / occurrence over several river regions.

The main advantages of the FRI and its variance S^2 FRI are: i) the association of a fish species with a certain river region is much more precisely described compared to the reference and accompanying species in the classical fish zonation, ii) species' preference for a certain river region is given together with its flexibility in using neighbouring river regions, iii) the index provides a species-specific life history trait, and iii) a species-specific qualifier for river zonation to be used as indicator for hydromorphologic integrity. Accordingly, all species get a river zonation qualifier and contribute to the assessment results, not only specialized or sensitive indicator species.

However, it must be emphasized that the FRI and the weighted probabilities of occurrence (Table 11) exclusively indicate the expected occurrence of a species in a certain river region, while they do not allow any conclusions about the species' abundance or dominance therein.

Based on the FRI characteristics of the single species in a given sample, survey or fish assemblage, the total FRI ($\text{FRI}_{\text{total}}$) can be calculated as average of the present species averages with unequal variances and random samples according to Sachs (1997) (Dußling et al. 2004, 2005):

$$\text{FRI}_{\text{total}} = \frac{\sum_{i=1}^S \left(\text{FRI}_i \frac{n_i}{S^2 \text{FRI}_i} \right)}{\sum_{i=1}^S \frac{n_i}{S^2 \text{FRI}_i}}$$

with FRI_i , $S^2 \text{FRI}_i$, n_i = FRI, variance, and number of specimens of species i .

The index value $\text{FRI}_{\text{total}}$ for the entire sample yields the coenotic classification of the fish assemblage surveyed according to the longitudinal functional process zones of river. Deviations from reference conditions are reflected as mismatch between the $\text{FRI}_{\text{total}}$ of the sample and the actual river section where it has been collected (Figure 12). Therefore, this index is able to detect different kind of hydromorphological degradations as far as they affect the natural longitudinal river characteristics and their related fish assemblage.

In Austria and Germany the FRI is still an element of the National fish-based assessment schemes (Schmutz et al. 2000, Dußling et al. 2004, 2005).

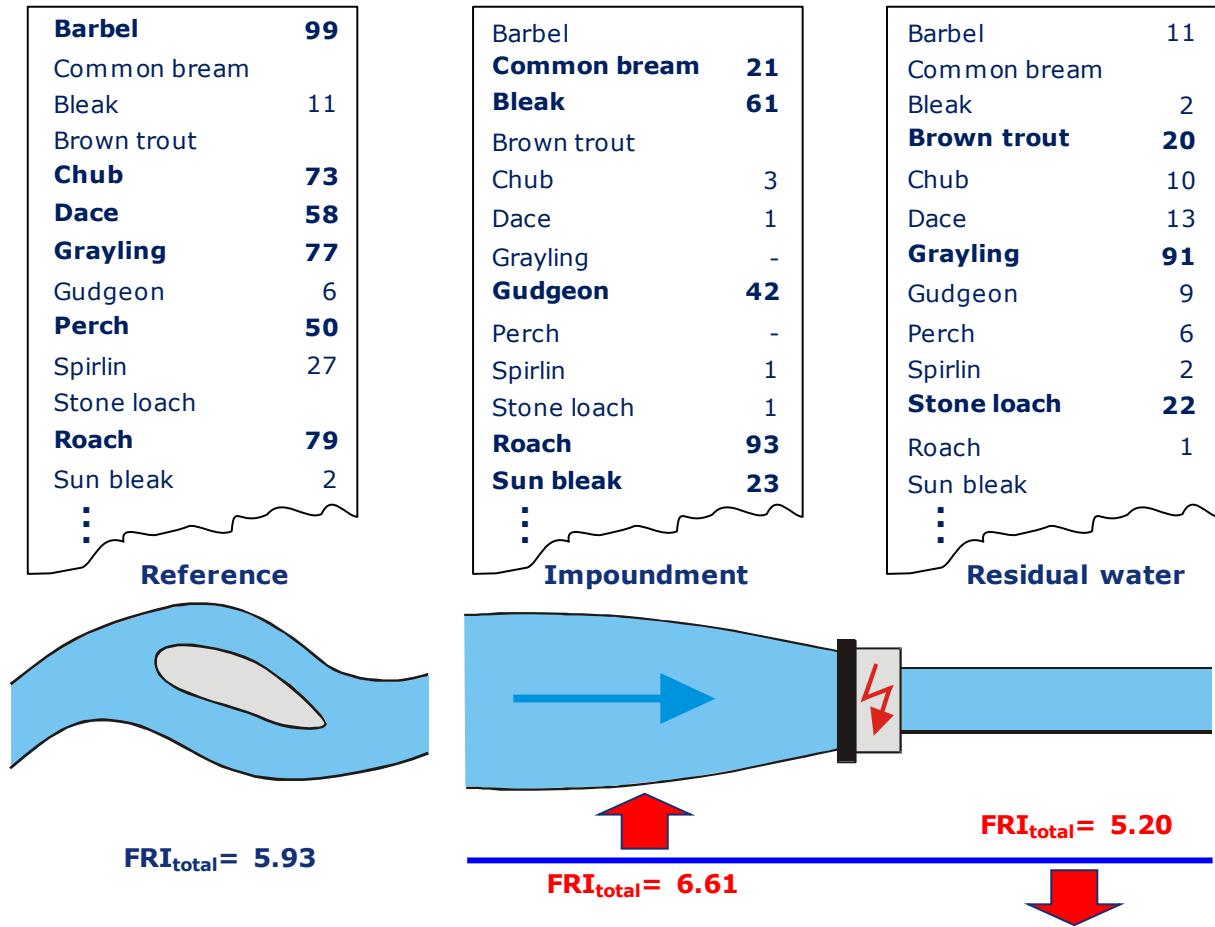


Figure 12 Example for the response of the total Fish Region Index (FRI_{total}) to hydromorphological alterations of a river stretch caused by damming; modified from Dußling et al. (2004).

5.4.2 Exemplary application of FRI

In a study of the effects of pressures at different spatial scales on the ecological potential of heavily modified water bodies in Germany a set of 142 fish sampling sites located in the federal state of Northrhine-Westphalia has been analysed (Kail & Wolter 2013). One side aspect of this study was the finding that a preliminary ordination analysis selected the FRI_{total} as fish metric which was related best to the anthropogenic pressures and which was together with the deficit in rheophilic fish abundance the only metric performing in all river types studied (Kail & Wolter 2013).

Based on this encouraging result the new harmonised fishes' FRIs have been applied for the first time on a European data set as preliminary test of the potential indicator value of FRI_{total} for hydromorphological degradation in various river types across the continent. The river fish intercalibration data set was used for first test runs of the differentiation potential of FRI_{total} without the data from Spain. For the other Member States permissions to use the data for indicator development within the REFORM project have been obtained from the national authorities. Thanks go to the Federal Agency for Water Management, Institute for Water Ecology, Fisheries and Lake Research, Mondsee, Landesamt für Natur,

Umwelt und Verbraucherschutz LANUV NRW, Fisheries Research Station of Baden-Württemberg, LAVES - Niedersächsisches Landesamt für Verbraucherschutz und Lebensmittelsicherheit, Landesamt für Umwelt, Naturschutz und Geologie Mecklenburg-Vorpommern, Bavarian State Research Center for Agriculture, Institute for Fishery, Environmental Assessment Department of the Lithuanian Environmental Protection Agency, EVA-Département Environnement et Agro-biotechnologies, Centre de Recherche Public – Gabriel Lippmann, Comenius University Bratislava, Swedish Agency for Marine and Water Management, and the Service public de wallonie, DGO3, Département de l'Etude du Milieu naturel et agricole (DEMNA), Direction Nature et Eau (D23 - DNE), Gembloux.

The data have been principally treated anonymous without referring to specific sites, region or countries. The fish abundance data given in the database were used to calculate the total Fish Region Index for each site using the formula given above. The potential river region of the sampling site has been roughly derived from the width and slope information given in the database using the classification of Huet (1949, 1953). This rather broad determination of the river region is still source of error and uncertainty; however, the majority of the sites should be correctly classified which seemed sufficient for first test runs. Information on hydromorphological pressures were used as given in the database but only linked to river region and FRI_{total} without georeferencing it.

The dataset finally plotted (Figure 13) yielded only hydromorphological pressures, river regions and the FRI_{total} values.

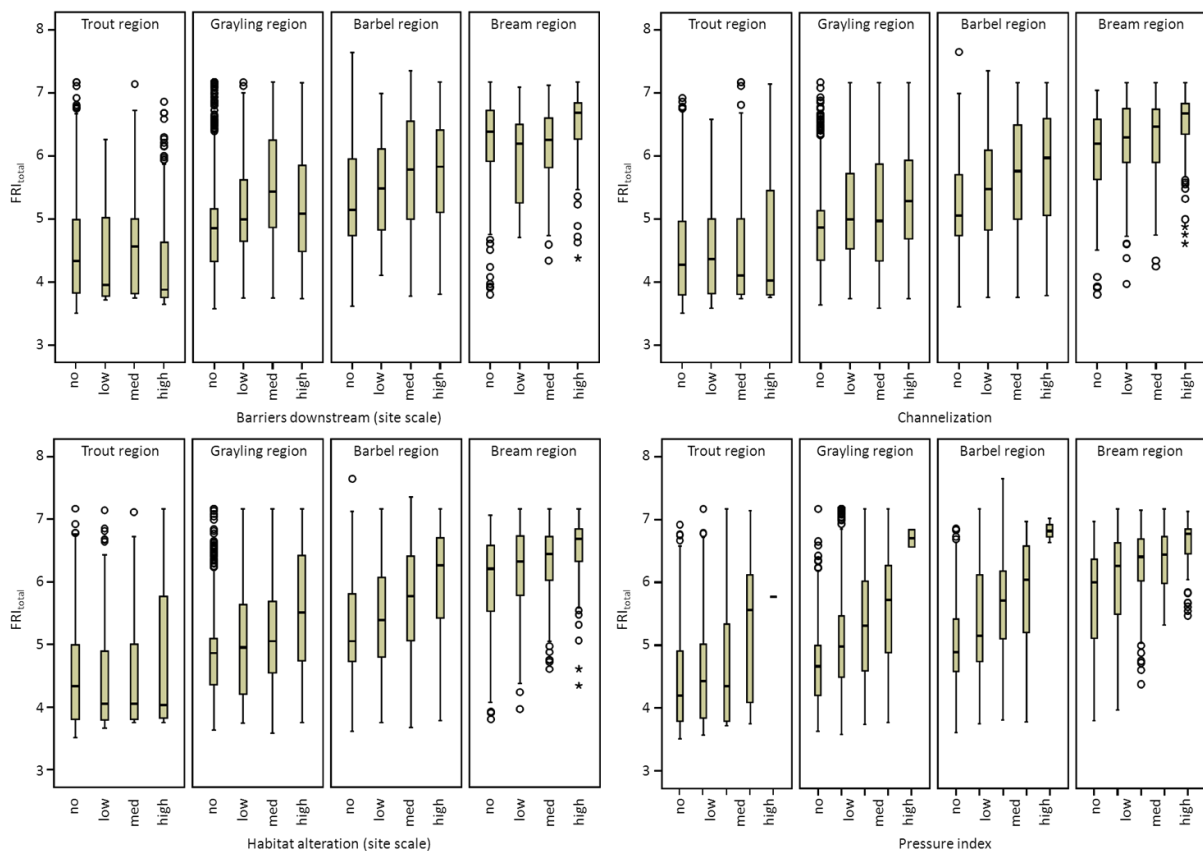


Figure 13 Response of the total Fish Region Index (FRI_{total}) at the site scale to selected hydromorphological pressures and a pressure index based on data from the river fish intercalibration dataset.

Although the data were not checked for correct classification of sites into river regions, the total FRI responded very plausible to increases of specific pressures within a river region (Figure 13). Best fits were obtained for the bream and barbel regions, while the performance in the trout region is rather poor. The latter was expected, because of the typically low number of species there and the limitations of the FRI_{total} metric for fish assemblages of less than ten species (Dußling et al. 2004). However, this doesn't matter, because the existing EFI+ index for fish-based assessments (<http://efi-plus.boku.ac.at/>) performs best exactly in the trout region and might be complemented by the FRI_{total} in the other river regions and particular in the lowlands.

The first results are very promising regarding the response of FRI_{total} to the different hydromorphological pressures especially in the larger river sections of the barbel and common bream regions and also in the lowland sections (Figure 13). Further a remarkably good correspondence has been obtained for the pressure index – as it was defined and categorised by the intercalibration group – between reference sites and non-reference sites for both good and high ecological status (Figure 14), despite the uncertainty of uncorrected site classifications in the dataset.

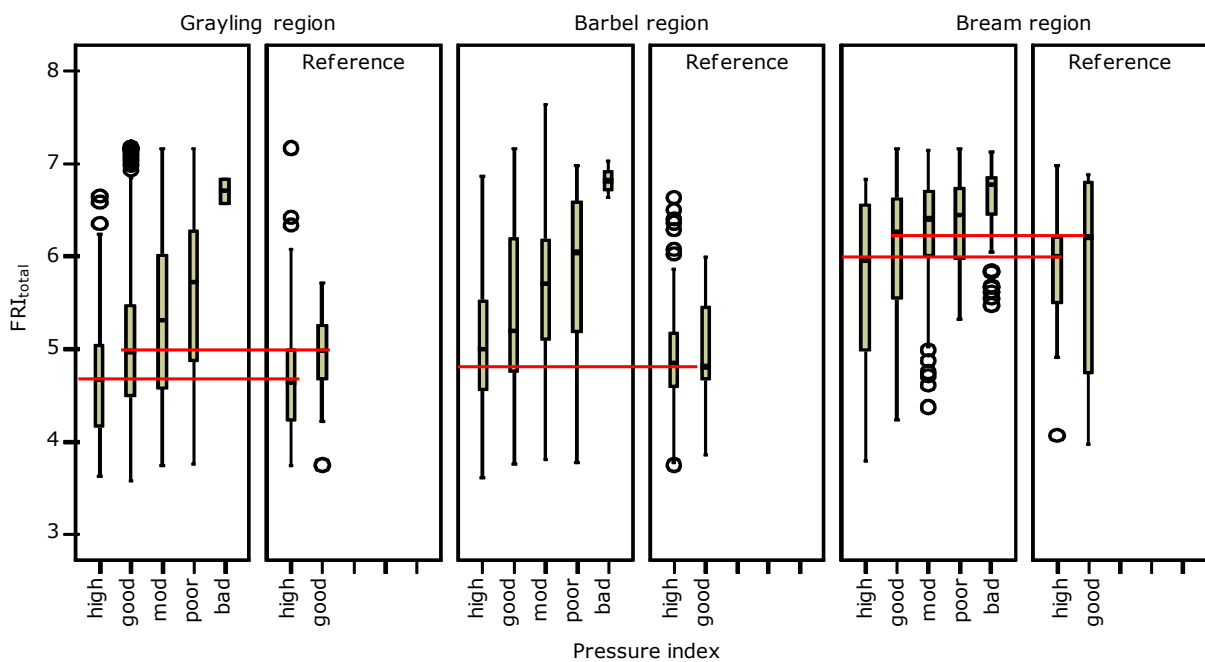


Figure 14 Comparison of the total Fish Region Index (FRI_{total}) between reference and non-reference sites for the pressure index based on data from the river fish intercalibration dataset. Red lines just illustrate correspondence.

Within the different workloads of REFORM there will be several new datasets collected and compiled which can be used to perform further detailed analyses of the FRI response to different hydromorphological pressures aiming in fine-tuning the FRI and improving its indicator value.

According to its preliminary performance, the FRI appears as an excellent candidate metric for fish-based assessment of pressure-specific hydromorphological degradation and improvement with the potential for intercalibration of assessment results at the European

scale. With the comparable classification of the regional species pools according to their preferred occurrence in the longitudinal river zones presented here (Table 11), the FRI based assessment results become comparable throughout varying species inventories.

5.5 Uncertainties

The following does not provide statistical analyses of uncertainties in the compiled data and obtained results. In contrast, it points on uncertainties due to insufficient data. The latter has been still often concluded (e.g. Smokorowski & Pratt 2007, Tyler et al. 2012, Comte et al. 2013, Elosegi & Sabater 2013, Isaak & Rieman 2013) but rarely addressed other than by even more sophisticated analyses of existing data (e.g. Azaele et al. 2009, Marmion et al. 2009, Grenouillet et al. 2011, Allan et al. 2012).

Most obvious was the lack of specific data on hydromorphologic variables and requirements, e.g. gravel calibre, which were needed for the identification and derivation of specific indicators for hydromorphological characteristics as well as to give advice for their successful rehabilitation and restoration. Still the ecological guild classification of fish refers to very few sentinel works only. For example, the classification of freshwater fish according to their spawning substrate requirements, which is commonly considered as the most sensitive ecological guild, is principally based on Balon's (1975, 1981) initial classification, while further studies on species' variety in spawning substrate selection or tolerances regarding this preference are widely absent (an exception is Zauner & Eberstaller 1999).

Applying for example the eco-ethological guild of lithophilic fish – gravel spawner with benthic larvae Balon (1975, 1981) – still raises questions for suitable gravel calibre, tolerated proportions of fines, egg depth, gravel permeability, and all the potential differences between species within this guild. Answering these questions is prerequisite for successful river restoration and rehabilitation of spawning sites for gravel spawners. However, the required data are still widely lacking. Within REFORM it was possible to collect specific data on gravel requirements for a total of 28 species out of 91 classified as lithophilic gravel spawner in the EFI+ database (<http://efi-plus.boku.ac.at/>). It seems rather uncertain how analogous their gravel quality requirements are compared to the species studied so far and considering the substantial interspecific differences observed (compare Chapter 5.1).

In addition most field surveys and investigations of environmental requirements have been performed in small rivers and headwaters and studied salmonids (e.g. Kondolf 2000, Smokorowski & Pratt 2007), most knowledge gaps exist for large rivers and non-salmonid species. This is also in accordance with the existing European fish data bases and fish-based assessment system. The majority of data and most of the less disturbed sites originate from headwaters and small rivers which created a significant bias towards trout streams. Not surprisingly that the fish-based assessment schemes in use so far perform best in river systems containing brown trout.

Beside the interspecific variation within guilds, the guild classification itself provides a substantial source of uncertainty due to the underlying basically expert judgment. The actually most widely used taxa and guild classification of European fish species has been compiled by the EFI+ consortium (<http://efi-plus.boku.ac.at/>). Within this project a total of 218 species was classified by 15 experts from Portugal to Romania and from UK / Fin-

land to Italy. Despite the very good spatial coverage of Europe and the probably larger national fish expert groups behind each expert, it seems still alarming that for one third of all species only one expert felt himself familiar enough to classify it (Figure 15). Another third of the European species got two or three expert opinions on their classification irrespective of the heterogeneity between the experts.

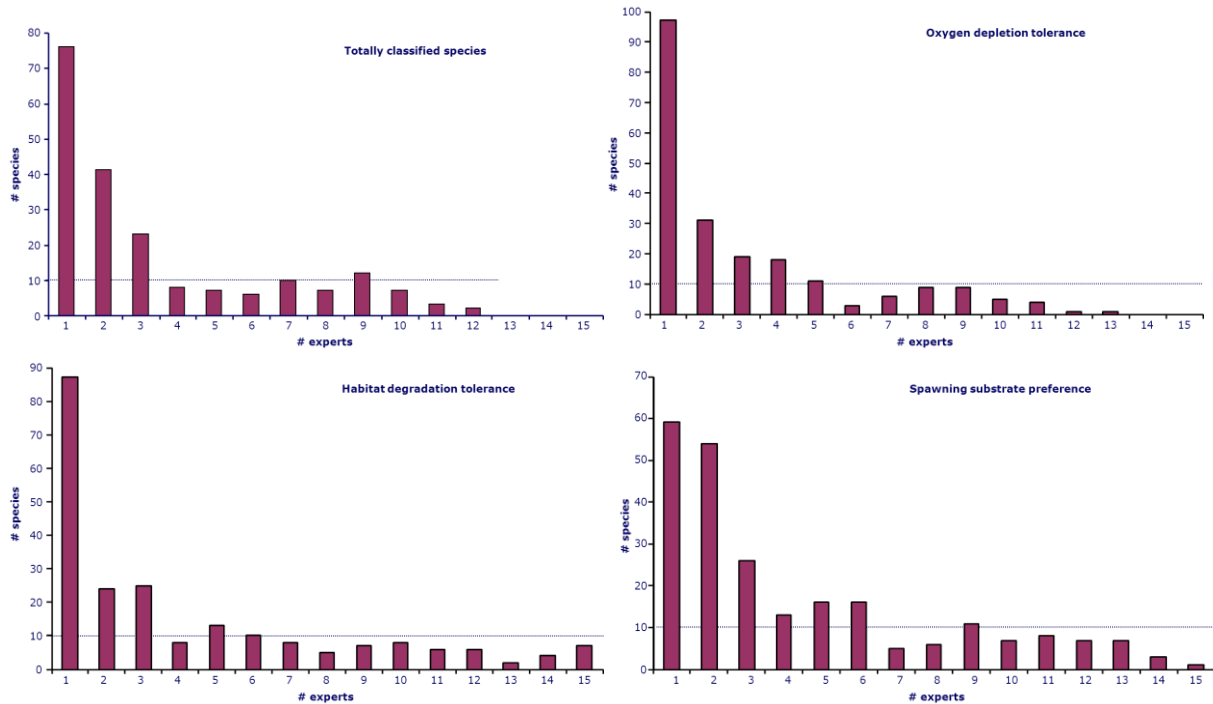


Figure 15 Expert opinions on the ecological classification of 218 European lamprey and fish species in total (upper left) and for anoxic tolerance (upper right), habitat degradation tolerance (lower left), and spawning substrate preference (lower right) in the EFI+ database (<http://efi-plus.boku.ac.at/>).

When looking at the more sensitive, hydromorphologically relevant guilds the knowledge situation is quite similar (Figure 15). Comparable few species seems well known among expert, while most of the species were classified by less than three experts throughout Europe. The latter was not explained by a high amount of endemic species in the database.

This rather insufficient knowledge on specific ecological requirements of species was not limited to European lampreys and freshwater fish species. A similar situation was found in aquatic macrophytes, where gravel sizes and flow velocity requirements have been obtained for 10 and 75 species, respectively, out of about 500 species (Chapter 3) and macroinvertebrates, where gravel sizes, flow velocity requirements, and shear stress were found for 56, 78, and 164 taxa, respectively, out of more than 20,000 known freshwater species (Chapter 4).

Well in line with the uncertainties and knowledge gaps mentioned here, Tyler et al. (2012) concluded a deep ignorance of the basic biology of a marine fauna and an urgent need for far greater efforts to compile biological trait data from their study of availability of biological traits data for 973 demersal marine species around the British Isles. Of eight

very basic biological traits (body size, diet, feeding mode, reproductive frequency, annual fecundity, larval development, adult movement, and adult life span) no data at all were found for 192 out of 825 invertebrate species and a full set of data just for 9% (88 taxa) of all species including fishes (Tyler et al. 2012).

Without doubt there are still a lot further of data and information around which have to be explored and analysed; however, there is also obvious evidence for the need to purposely collect new data and to design straightforward experiments to fill the gaps in ecological knowledge and to provide the scientific basis for successful river rehabilitation.

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7 Appendices

Table 5 Preferred flow velocities of macrophytes (PS= photosynthesis).

Species	Velocity (m/s) of occurrence	Velocity (m/s) of highest abundance	Ecological property	Comments	Study
<i>Apium nodiflorum</i>	0.31-0.69				6
<i>Azolla filiculoides</i>	<0.69	0			17
	almost 0	0			16
<i>Berula erecta</i>			rheobiont		14
	0.31-0.69				6
<i>Butomus umbellatus</i>	<0.69	0.05-0.3			17
<i>Callitriche sp.</i>	0.31-0.69	0.31-0.69			17
<i>Callitriche hamulata</i>	0.05-0.3	0.05-0.3	rheobiont		17
					14
<i>Callitriche hermaphroditica</i>	0-0.4	0-0.2			12
<i>Callitriche platycarpa</i>			rheophil		14
<i>Callitriche stagnalis</i>			rheophil		14
	>0.0008			minimum for saturated PS	3
<i>Carex acutiformes</i>	almost 0				6
<i>Ceratophyllum demersum</i>		0			17
	0-0.2	0-0.2			12
	almost 0				6
<i>Chara sp.</i>	0-0.6	0.2-0.4			12
<i>Cinclidotus riparius</i>		>0.7			17
<i>Cinclidotus fontinaloides</i>		>0.7			17
<i>Cratoneuron filicinum</i>		>0.7			17
<i>Egeria densa</i>	0-1				16
<i>Eichhornia crassipes</i>	0.05-0.3	0.05-0.3			17
<i>Elodea canadensis</i>			rheotolerant		14
	0.31-0.69	0.31-0.69			17
	0-0.4	0-0.2			12
	almost 0				6
<i>Elodea nuttallii</i>	<0.69	0			17
			rheotolerant		14
<i>Fissidens rufulus</i>	>0.7	>0.7			17
<i>Fontinalis antipyretica</i>		>0.7			17
			rheobiont		14
<i>Fontinalis hypnoides</i>	<0.3	0			17
<i>Glyceria maxima</i>	almost 0				6
<i>Groenlandia densa</i>			rheophil		14
<i>Hippuris vulgaris</i>			rheophil		14
<i>Hydrocharis morsus-ranae</i>	<0.3	0.05-0.3			17
<i>Hygroamblystegium fluviatile</i>	<0.3	0			17
<i>Hygroamblystegium tenax</i>	<0.3	0.05-0.3			17
<i>Hygrohypnum eugyrium</i>	0	0			17
<i>Hygrohypnum luridum</i>	<0.69	0			17
<i>Isolepis fluitans</i>			rheobiont		14
<i>Lemna sp.</i>			rheophob		14
<i>Lemna minor</i>		0			17
	almost 0				6
<i>Lemna minuta</i>	almost 0	0			16
<i>Lemna turionifera</i>	0.05-0.3	0.05-0.3			17
<i>Leptodictyum riparium</i>	0.31-0.69	0.31-0.69			17
Mosses	>0.6	>0.6			12
<i>Myriophyllum alterniflorum</i>			rheobiont		14
<i>Myriophyllum aquaticum</i>	0-0.3				16

Species	Velocity (m/s) of occurrence	Velocity (m/s) of highest abundance	Ecological property	Comments	Study
(emerged)					
<i>Myriophyllum aquaticum</i> (submerged)	0.4-1				16
<i>Myriophyllum exalbescens</i>	0-0.4	0-0.2			12
<i>Myriophyllum spicatum</i>		0			17
			rheobiont		14
	0.31-0.69				6
<i>Myriophyllum verticillatum</i>	0	0			17
<i>Najas marina</i>		0			17
<i>Najas minor</i>		0			17
<i>Nasturtium officinale</i>			rheophil		14
<i>Nitellopsis obtusa</i>	<0.3	0			17
<i>Nuphar lutea</i>			rheotolerant		14
	0.05-0.3	0.05-0.3			17
	<0.3				6
<i>Nymphaea alba</i>			rheophob		14
<i>Persicaria amphibia</i>	0	0			17
<i>Platyhyponidium riparioides</i>	0.31-0.69				19
<i>Potamogeton acutifolius</i>	<0.3	0			17
<i>Potamogeton berchtoldii</i>	0-0.4	0-0.2			12
<i>Potamogeton crispus</i>		0.05-0.3			17
			rheophil		14
<i>Potamogeton friesii</i>	0	0			17
<i>Potamogeton gramineus</i>	<0.69	0.05-0.3			17
	0-0.4	0-0.4			12
<i>Potamogeton lucens</i>	<0.25				14
	<0.3	0			17
<i>Potamogeton natans</i>		>0.7			16
<i>Potamogeton nodosus</i>		0			17
<i>Potamogeton pectinatus</i>			rheobiont		14
		>0.7			16
	<0.3				6
	0-0.4	0-0.2			12
	>0.0004			minimum for saturated PS	9
<i>Potamogeton perfoliatus</i>	<0.69	0			17
			rheophil		14
<i>Potamogeton pusillus</i>	<0.69	0.31-0.69			17
<i>Potamogeton richardsonii</i>	0-0.4	0-0.2			12
<i>Potamogeton x zizii</i>	<0.3	0			17
<i>Ranunculus aquatilis</i>	0-0.6	0.4-0.6			12
<i>Ranunculus circinatus</i>			rheotolerant		14
<i>Ranunculus fluitans</i>	0.25-1.2		rheobiont		14
	>0.31	0.31-0.69			17
<i>Ranunculus peltatus</i>	0-0.05		rheobiont		14
<i>Ranunculus pseudofluitans</i>	>0.005			minimum for saturated PS	3
<i>Ranunculus penicillatus</i>			rheobiont		14
	<0.45				8
	>0.05			minimum for saturated PS	8
<i>Ranunculus trichophyllus</i>			rheobiont		14
<i>Rhynchosstegium riparioides</i>		>0.7			17
<i>Sagittaria sagittifolia</i>			rheotolerant		14
	0				6
<i>Salvinia natans</i>		0			17
<i>Schistidium rivulare</i>	0	0			17
<i>Schoenoplectus lacustris</i>	<0.3				6

Species	Velocity (m/s) of occurrence	Velocity (m/s) of highest abundance	Ecological property	Comments	Study
<i>Sparganium emersum</i>	<0.3		rheotolerant		14
<i>Sparganium erectum</i>	<0.3				6
<i>Spirodela polyrhiza</i>		0	rheophob		6
<i>Stuckenia amblyphylla</i>	>0	0.35-0.65			17
<i>Stuckenia pectinata</i>		0			14
<i>Thalassia testudinum</i>	>0.05			minimum for saturated PS	18
<i>Trapa natans</i>	<0.3	0			17
<i>Utricularia vulgaris</i>	0	0			17
<i>Vallisneria americana</i>	<0.07				13
<i>Vallisneria spiralis</i>		0			17
<i>Wolffia arrhiza</i>	0.05-0.3	0.05-0.3			16
<i>Zannichellia palustris</i>		>0.7	rheophob		17
	<0.5				14
<i>Zostera marina</i>	>0.03		rheophil	minimum for saturated PS	2
	>0.16				14
	<0.5				15
	<1.2				10
	<1.5				1
	<1.8				4
					7
					5

Studies: 1= Conover (1964), 2= Sculthorpe (1967), 3= Westlake (1967), 4= Scoffin (1970), 5= Phillips (1974), 6= Haslam (1978), 7= Fonseca et al. (1982), 8= Werner & Weise (1982), 9= Madsen & Søndergaard (1983), 10= Fonseca & Kenworthy (1987), 11= Koch (1994), 12= French & Chambers (1996), 13= Merrell (1996), 14= Pott & Remy (2000), 15= Koehl, cited in Koch (2001), 16= Hussner & Lössch (2005), 17= Janauer et al. (2010), 18= Nowak & Nobis (2012), 19= Gecheva et al. (2013)

Table 6 Preferred substrata of macrophytes (*only the most preferred substrate of several is listed).

Species	Substrate	Size (µm)	Organic content	Study
<i>Alisma triviale</i>	sand / gravel			2*
<i>Apium nodiflorum</i>	sand / gravel			1
<i>Berula erecta</i>	sand / gravel			1
<i>Brasenia schreberi</i>	sand / gravel			2*
<i>Calla palustris</i>	sand / gravel			2*
<i>Callitriche sp.</i>	sand / gravel			1, 2*
<i>Callitriche hermaphroditica</i>	silt / sand	14-470		4
<i>Caltha palustris</i>	sand / gravel			2*

Species	Substrate	Size (µm)	Organic content	Study
<i>Carex acutiformes</i>	peat			1
<i>Ceratophyllum demersum</i>	peat			1
	silt	14-56		4
	sand / gravel			2*
<i>Chara sp.</i>	sand	63-470		4
	sand / gravel			2*
<i>Egeria densa</i>			detritus	7*
	fine		low	7*
<i>Eleocharis sp.</i>	sand / gravel			2*
<i>Elodea canadensis</i>	peat			1
	sand / small gravel			6
	silt	14-56		4
	sand / gravel			2*
<i>Fontinalis dalecarlica</i>	boulders			8
<i>Glyceria maxima</i>	peat			1
<i>Hippuris vulgaris</i>	sand / gravel			2*
<i>Hydrilla sp.</i>			<5%	5
<i>Hygrohypnum ocraceum</i>	boulders			8
<i>Lemna minor</i>	peat			1
	sand / gravel			2*
<i>Lemna trisulca</i>	sand / gravel			2*
<i>Megalodonta beckii</i>	sand / gravel			2*
<i>Mentha arvensis</i>	sand / gravel			2*
Mosses	stones / rocks			1
	bare rocks			4
<i>Myriophyllum aquaticum (emerged)</i>			detritus	7*
	fine		low	7*
<i>Myriophyllum aquaticum (submerged)</i>	sand / gravel			7*
<i>Myriophyllum exalbescens</i>	silt	14-56		4
	sand / gravel			2*
<i>Myriophyllum spicatum</i>	sand / gravel			1
	clay			8
<i>Myriophyllum triphyllum</i>	sand			8
	sand / small gravel			6
<i>Myriophyllum verticillatum</i>			high	2*
<i>Najas flexilis</i>	sand / gravel			2*
<i>Nuphar lutea</i>	mud / silt			1
<i>Nuphar microphyllum</i>	sand / gravel			2*
<i>Nuphar variegatum</i>	sand / gravel			2*

Species	Substrate	Size (µm)	Organic content	Study
<i>Nymphaea odorata</i>	sand / gravel			2*
<i>Nymphaea tetragona</i>	sand / gravel			2*
<i>Nymphaea tuberosa</i>	clay / sand / gravel			2*
<i>Phragmites australis</i>	peat			1
<i>Platyhyponidium riparioides</i>	coarse			10
<i>Polygonum amphibium</i>	peat			1
	sand / gravel			2*
<i>Potamogeton alpinus</i>	sand / gravel			2*
<i>Potamogeton amplifolius</i>	sand / gravel			2*
<i>Potamogeton berchtoldii</i>	silt / sand	14-470		4
<i>Potamogeton cheesemanii</i>	sand			8
	sand / small gravel			6
<i>Potamogeton epihydrus</i>	sand / gravel			2*
<i>Potamogeton filiformis</i>	sand / gravel			2*
<i>Potamogeton foliosus</i>	sand / gravel			2*
<i>Potamogeton friesii</i>	sand / gravel			2*
<i>Potamogeton gramineus</i>	silt	14-56		4
	sand / gravel			2*
<i>Potamogeton natans</i>	peat			1
	sand / gravel			2*
<i>Potamogeton nodosus</i>			<5%	5
<i>Potamogeton obtusifolius</i>	sand / gravel		high	2*
				2*
<i>Potamogeton pectinatus</i>	mud / silt			1
	clay			8
	silt	14-56		4
	sand / gravel			2*
			<26 mg C g ⁻¹	5
<i>Potamogeton perfoliatus</i>	mud / silt			1
<i>Potamogeton praelongus</i>	sand / gravel			2*
<i>Potamogeton pusillus</i>	sand / gravel			2*
<i>Potamogeton richardsonii</i>	silt	14-56		4
	sand / gravel			2*
<i>Potamogeton robbinsii</i>	sand / gravel			2*
<i>Potamogeton spirillus</i>	sand / gravel			2*
<i>Potamogeton vaginatus</i>	sand / gravel			2*
<i>Potamogeton zosteriformis</i>	sand / gravel			2*
<i>Ranunculus sp.</i>	sand / gravel			1

Species	Substrate	Size (µm)	Organic content	Study
<i>Ranunculus aquatilis</i>	sand	63-470		4
	silt / clay	<830	high	3
	sand / gravel			2*
<i>Ranunculus trichophyllus</i>	sand			8
	gravel / cobble			6
<i>Riccis fluitans</i>	sand / gravel			2*
<i>Rorippa nasturtium-aquaticum</i>	sand / gravel			1
<i>Ruppia maritime</i>	sand / gravel			2*
<i>Sagittaria sp.</i>	sand / gravel			2*
<i>Sagittaria rigida</i>	sand / gravel			2*
<i>Sagittaria sagittifolia</i>	mud / silt			1
<i>Schoenoplectus lacustris</i>	sand / gravel			1
<i>Sium suave</i>	sand / gravel			2*
<i>Sparganium sp.</i>	sand / gravel			2*
<i>Sparganium emersum</i>	sand / gravel			1
<i>Sparganium erectum</i>	sand / gravel			1
<i>Spirodela polyrhiza</i>	sand / gravel			2*
<i>Stuckenia amblyphylla</i>	silt		distinctly organic	9*
<i>Utricularia intermedia</i>	clay / sand / gravel			2*
<i>Utricularia minor</i>			high	2*
<i>Utricularia vulgaris</i>	sand / gravel			2*
<i>Vallisneria americana</i>			<6.5%	5
<i>Vallisneria spiralis</i>			detritus	7*
	fine sand		low	7*
				7*
<i>Zizania aquatic</i>	sand / gravel			2*
<i>Zosterella dubia</i>	sand / gravel			2*

Studies: 1= Haslam (1978), 2= Pip (1979)*, 3= Boeger (1992), 4= French & Chambers (1996), 5= Koch (2001), 6= Riis & Biggs (2003), 7= Hussner & Lösch (2005)*, 8= Lacoul & Freedman 2006, 9= Nowak & Nobis (2012)*, 10= Gecheva et al. (2013)

Table 7 Substrate and grain size preferences of selected benthic invertebrates; n.d.= no differentiation; sources: 1= (Tolkamp 1982), 2= (Singh et al. 2010).

Species	Season	Preferred substrate	Preferred grain size (mm)	Study
Bivalvia				
<i>Pisidium</i> sp.	n. d.	very fine sand, medium sand, very coarse sand	0.05 – 0.125, 0.25 – 0.5, 1 – 2	1
Clitellata				
<i>Eiseniella tetraeda</i>	n. d.	medium gravel-cobbles	4 – 128	1
Coleoptera				
<i>Agabus</i> larvae	n. d.	coarse detritus, leaves		1
<i>Dryops</i> sp.	Winter	Very coarse sand	1 – 2	2
<i>Elmis aena</i>	n. d.	medium gravel, small pebbles – cobbles	4 – 8, 16 – 128	1
<i>Helodes</i> larvae	n. d.	detritus, coarse detritus, leaves		1
<i>Hydrophilus</i> sp.	Spring-Summer	no preference		2
<i>Promoresia</i> sp.	Winter	no preference		2
	Spring	very coarse sand	1 – 2	2
	Summer	cobbles	128 – 256	2
	Autumn	no preference		2
<i>Psephenus</i> sp.	Winter	very coarse sand	1 – 2	2
	Spring	no preference		2
	Summer	cobbles	128 – 256	2
	Autumn	fine gravel	2 – 4	2
Crustacea				
<i>Gammarus pulex</i>	n. d.	very coarse sand, detritus, coarse detritus, leaves	1 – 2	1
Diptera				
<i>Antocha</i> sp.	Winter	no preference		2
	Spring	very coarse sand	1 – 2	2
	Summer	cobbles	128 – 256	2
	Autumn	fine gravel	2 – 4	2
<i>Apsectrotanypus trifacip.</i>	n. d.	fine – medium sand, medium gravel, large pebbles, leaves	0.125 – 0.50, 4 – 8, 32 – 64	1
<i>Atherix</i> sp.	Winter	no preference		2
	Spring	fine gravel	2 – 4	2
	Summer	cobbles	128 – 256	2
	Autumn	no preference		2
<i>Bibiocephala</i> sp.	Winter	very coarse sand	1 – 2	2
	Spring	cobbles	128 – 256	2
	Summer	cobbles	128 – 256	2
	Autumn	no preference		2
<i>Brillia modesta</i>	n. d.	detritus, coarse detritus, leaves		1
<i>Chaetocladius</i> sp.	n. d.	fine – coarse gravel	2 – 16	1
<i>Chironomini</i> ssp.	n. d.	very coarse sand	1 – 2	1
<i>Chironomini</i> pupae ssp.	n. d.	coarse detritus, leaves		1

Species	Season	Preferred substrate	Preferred grain size (mm)	Study
<i>Chironomus sp.</i>	Winter	no preference		2
	Spring	very coarse sand	1 – 2	2
	Summer	cobbles	128 – 256	2
	Autumn	no preference		2
<i>Conchapelopia melanops</i>	n. d.	detritus, coarse detritus, leaves		1
<i>Corynoneura ssp.</i>	n. d.	coarse detritus, leaves		1
<i>Dicranota sp.</i>	n. d.	medium gravel	4 – 8	1
<i>Diplocladius cultriger</i>	n. d.	detritus, leaves		1
<i>Eukiefferiella gr. discol.</i>	n. d.	coarse detritus, leaves		1
<i>Hexatoma sp.</i>	Winter	no preference		2
	Spring	fine gravel	2 – 4	2
	Summer	no preference		2
	Autumn	fine gravel	2 – 4	2
<i>Limnophila sp.</i>	n. d.	very fine sand, medium sand, medium gravel, large pebbles	0.05 – 0.125, 0.25 – 0.50, 4 – 8, 32 – 64	1
<i>Macropelopia nebulosa</i>	n. d.	fine sand, very coarse sand, medium – coarse gravel	0.125 – 0.25, 1 – 2, 4 – 16	1
<i>Micropsectra gr. praecox</i>	n. d.	very fine – fine sand, detritus, coarse detritus, leaves	0.05 – 0.25	1
<i>Orthocladus sp.</i>	n. d.	coarse gravel – small pebbles	8 – 32	1
<i>Palpomyia sp.</i>	n. d.	very fine sand, medium sand, coarse detritus	0.05 – 0.125, 0.25 – 0.5	1
<i>Polypedilum brevantennat.</i>	n. d.	very fine sand – medium sand	0.05 – 0.50	1
<i>Polypedilum laetum</i>	n. d.	very coarse sand, medium gravel coarse detritus, leaves	1 – 2, 4 – 8	1
<i>Procladius sp.</i>	n. d.	fine – medium sand	0.125 – 0.50	1
<i>Prodiamesa olivacea.</i>	n. d.	very fine – medium sand, coarse detritus, leaves	0.05 – 0.50	1
<i>Ptychoptera sp.</i>	n. d.	very fine sand, medium sand	0.05 – 0.125, 0.25 – 0.50	1
<i>Rheocricotopus sp.</i>	n. d.	coarse detritus, leaves		1
<i>Rheotanytarsus sp.</i>	n. d.	very coarse sand, medium gravel, coarse detritus	1 – 2, 4 – 8	1
<i>Simulium latipes</i>	n. d.	coarse detritus, leaves		1
<i>Simulium sp.</i>	Winter	medium gravel	4 – 8	2
	Spring	no preference		2
	Summer	cobbles	128 – 256	2
	Autumn	no preference		2
<i>Stictochironomus sp.</i>	n. d.	fine – coarse sand	0.125 – 1	1
<i>Tanytarsus sp.</i>	n. d.	fine sand, very coarse sand, medium gravel, large pebbles	0.125 – 0.25, 4 – 8, 32 – 64	1

Species	Season	Preferred substrate	Preferred grain size (mm)	Study
<i>Zavrelimyia</i> sp.	n. d.	fine sand, detritus, leaves	0.125 – 0.25	1
Ephemeroptera				
<i>Baetis vernus</i> .	n. d.	fine sand, large pebbles	0.125 – 0.25, 32 – 64	1
<i>Baetis</i> sp.	Winter	very coarse sand	1 – 2	2
	Spring	cobbles	128 – 256	2
	Summer	very coarse sand, cobbles	1 – 2, 128 – 256	2
<i>Caenis</i> sp.	Autumn	no preference		2
	Winter - Spring	no preference		2
	Summer	cobbles	128 – 256	2
<i>Cynigma</i> sp.	Autumn	cobbles	128 – 256	2
	Winter	medium gravel	4 – 8	2
<i>Ephemerella</i> sp.	Spring - Autumn	no preference		2
	n. d.	fine – medium sand, medium gravel – small pebbles	0.125 – 0.50, 4 – 32	1
<i>Ephemerella</i> sp.	Winter	no preference		2
	Spring	very coarse sand, cobbles	1 – 2, 128 – 256	2
	Summer	medium gravel, very coarse sand	4 – 8, 128 – 256	2
	Autumn	cobbles	128 – 256	2
<i>Heptagenia</i> sp.	Winter	medium gravel	4 – 8	2
	Spring	cobbles	256 – 512	2
	Summer	cobbles	128 – 256	2
	Autumn	fine gravel	2 – 4	2
<i>Rithrogena</i> sp.	Winter	very coarse sand	1 – 2	2
	Spring	cobbles	256 – 512	2
	Summer	no preference		2
	Autumn	very coarse sand	1 – 2	2
Hemiptera				
<i>Hesperocorixa</i> sp.	Winter - Summer	no preference		2
	Autumn	very coarse sand	1 – 2	2
Hydracarina				
<i>Hydracarina</i> ssp.	n. d.	medium – coarse sand	0.25 – 1	1
Lepidoptera				
<i>Bellura</i> sp.	Autumn	very coarse sand	1 – 2	2
<i>Nymphula</i> sp.	Winter - Spring	no preference		2
	Summer	cobbles	128 – 256	2
	Autumn	very coarse sand	1 – 2	2
Megaloptera				
<i>Corydalus</i> sp.	Winter	no preference		2
	Spring	very coarse sand	1 – 2	2
	Summer	cobbles	128 – 256	2

Species	Season	Preferred substrate	Preferred grain size (mm)	Study
	Autumn	no preference		2
Odonata				
<i>Hagenius sp.</i>	Winter - Summer	no preference		2
	Autumn	fine gravel	2 – 4	2
Oligochaeta				
<i>Oligochaeta ssp.</i>	n. d.	very fine – fine sand, coarse sand	0.05 – 0.25, 0.5 – 1	1
Plecoptera				
<i>Amphinemura standfussi.</i>	n. d.	large pebbles, leaves	32 – 64	1
<i>Isoperla sp.</i>	Winter	fine gravel	2 – 4	2
	Spring	cobbles	256 – 512	2
	Summer	cobbles	128 – 256	2
	Autumn	fine gravel	2 – 4	2
<i>Perla sp.</i>	Winter - Spring	no preference		2
	Summer	cobbles	128 – 256	2
	Autumn	no preference		2
<i>Nemoura cinerea</i>	n. d.	leaves		1
Trichoptera				
<i>Chaetopteryx villosa</i>	n. d.	small – large pebbles, coarse detritus	16 – 64	1
<i>Glossosoma sp.</i>	Winter	no preference		2
	Spring	very coarse sand	1 – 2	2
	Summer	coarse gravel, cobbles	8 – 16, 128 – 256	2
	Autumn	fine gravel	2 – 4	2
<i>Hydropsyche sp.</i>	Winter	very coarse sand	1 – 2	2
	Spring	very coarse sand	1 – 2	2
	Summer	cobbles	128 – 256	2
	Autumn	very coarse sand	1 – 2	2
<i>Limnephilus sp.</i>	Winter	very coarse sand	1 – 2	2
	Spring	no preference		2
	Summer	coarse gravel, cobbles	8 – 16, 128 – 256	2
	Autumn	fine gravel	2 – 4	2
<i>Lithax obacurus</i>	n. d.	very coarse sand, fine gravel, coarse gravel – cobbles	1 – 4, 8 – 128	1
<i>Micropterna saquax</i>	n. d.	medium gravel, leaves	4 – 8	1
<i>Nectopsyche (Leptocella) sp.</i>	Winter	very coarse sand	1 – 2	2
	Spring	cobbles	128 – 256	2
	Summer	coarse gravel, cobbles	8 – 16, 128 – 256	2
	Autumn	no preference		2
<i>Philopotomus sp.</i>	Winter	very coarse sand	1 – 2	2
	Spring	very coarse sand	1 – 2	2
	Summer	cobbles	128 – 256	2
	Autumn	very coarse sand, cobbles	1 – 2, 128 – 256	2
<i>Plectrocnemia conspersa</i>	n. d.	coarse detritus, leaves		1
<i>Rhyacophila sp.</i>	Winter	no preference		2

Species	Season	Preferred substrate	Preferred grain size (mm)	Study
<i>Sericostoma personatum</i>	Spring	fine gravel	2 – 4	2
	Summer	no preference		2
	Autumn	cobbles	128 – 256	2
	n. d.	very coarse sand – small pebbles, coarse detritus	1 – 32	1

Table 8 Hydraulic preferences of selected benthic invertebrates. (a)= adult, (l)= larvae, FST= average hemisphere number, R²= strength of the average taxa preference model; shear stresses calculated according to Statzner et al. (1991); ind= indifferent, lip= limnophil, lrh= limnorheophil, rlp= rheolimnophil, rhp= rheophil, rhb= rheobionte; references: 1= Mérigoux et al. (2009), 2= Dolédec et al. (2007), 3= Euro-limpacs Consortium (2009), 4= Schmedtje (1995), 5= Brabec et al. (2007), 6= Buffagni et al. (2007), 7= Graf et al. (2007), 8= Graf et al. (2006).

Species	R ²	FST	Shear Stress	Current preference
Bivalvia				
Corbiculidae				
<i>Corbicula fluminea</i>	0.01	7.95	(1) 0.39	rlp (3)
Dreissenidae				
<i>Dreissena polymorpha</i>	0.25	12.26	(1) 1.16	ind (3)
Sphaeriidae				
<i>Pisidium</i> spp.	0.05	6.57	(1) 0.25	
	0.17	5.85	(1) 0.21	
	0.22	5.47	(2) 0.19	
Coleoptera				
Dytiscidae				
<i>Oreodytes sanmarkii</i> (a)	0.27	5.62	(2) 0.2	rhp (3)
<i>Oreodytes sanmarkii</i> (l)	0.53	4.06	(2) 0.14	rhp (3)
<i>Platambus maculatus</i>	0.51	3.42	(2) 0.13	rlp (3)
Elmidae				
<i>Elmis aenea</i> (a)	0.15	11.44	(2) 0.95	rhp (3)
<i>Elmis aenea</i> (l)	0.11	8.64	(2) 0.48	rhp (3)
<i>Elmis latreillei</i> (a)	0.66	12.15	(2) 1.13	rhp (3)
<i>Elmis</i> spp.	0.49	13.22	(1) 1.65	
<i>Elmis</i> spp. (l)	0.1	8.82	(2) 0.5	
<i>Esolus angustatus</i> (a)	0.5	10.26	(2) 0.66	rhb (3)
<i>Esolus</i> spp.	0.32	11.57	(1) 0.98	
<i>Esolus</i> spp. ad	0.25	12.1	(1) 1.12	
<i>Esolus</i> spp. (l)	0.13	8.52	(2) 0.46	
<i>Limnius perrisi</i> (a)	0.04	8.63	(2) 0.48	rhb (3)
<i>Limnius</i> spp.	0.19	11.52	(1) 0.97	
<i>Limnius</i> spp. (l)	0.13	8.18	(2) 0.42	
<i>Limnius volckmari</i> (a)	0.09	9.13	(2) 0.54	rhp (3)
<i>Limnius volckmari</i> (l)	0.04	9.46	(2) 0.57	rhp (3)
<i>Orectochilus villosus</i>	-0.01	8.39	(1) 0.45	rhp (3)
	0.06	7.87	(2) 0.38	rhp (3)
<i>Oulimnius</i> spp.	0.14	10.77	(1) 0.79	rlp (3)
<i>Riolus cupreus</i>	0.01	7.94	(2) 0.39	rhp (3)
Haliplidae				
<i>Brychius elevatus</i> (a)	0.12	6.08	(2) 0.22	rhp (3)

Species	R ²	FST	Shear Stress	Current preference
<i>Brychius elevatus</i> (l)	0.05	7.7 (2)	0.36	rhp (3)
Hydraenidae				
<i>Hydraena gracilis</i>	0.28	11.96 (2)	1.08	rhp (3)
<i>Hydraena minutissima</i>	0.22	11.23 (2)	0.9	rhp (3)
Crustacea				
Asellidae	0.2	5.73 (1)	0.2	
<i>Asellus aquaticus</i>	0.1	6.43 (1)	0.24	ind (3)
	0.09	6.86 (2)	0.26	
Gammaridae				
<i>Echinogammarus beriloni</i>	0.48	8.2 (2)	0.42	rlp (3)
<i>Gammarus fossarum</i>	0.03	8.72 (1)	0.49	rhp (3)
	0.23	7.91 (2)	0.39	
<i>Gammarus pulex</i>	0.01	9.46 (1)	0.57	rhp (3)
	0.27	7.64 (2)	0.35	
<i>Gammarus</i> spp.	0.05	9.18 (1)	0.55	
	0.4	8.57 (2)	0.47	
Diptera				
Limoniidae	0.04	9.93 (1)	0.62	
<i>Antocha</i> spp.	0.05	8.87 (2)	0.51	
<i>Hexatoma</i> spp.	0.09	7.29 (2)	0.31	lip (4)
<i>Molophilus</i> spp.	0.18	6.97 (2)	0.27	lip (4)
Athericidae				
<i>Atherix ibis</i>	0.22	9.84 (2)	0.61	rhp (3)
<i>Athrichops crassipes</i>	0.12	6.19 (2)	0.23	rhb (3)
<i>Ibisia marginata</i>	0.05	8.24 (2)	0.43	
Ceratopogonidae				
<i>Bezzia</i> spp.	0.08	10 (2)	0.63	rhp (4)
Ceratopogoninae	0.08	7.1 (1)	0.28	
	0.06	8.7 (2)	0.49	
Chironomidae	0.12	9.18 (2)	0.55	
Chironomini	0.38	5.84 (1)	0.21	
Orthoclaadiinae	0.1	9.84 (1)	0.61	
<i>Rheotanytarsus</i> spp.	0.18	5.98 (2)	0.22	rhp (5)
Tanypodinae	0	9.37 (1)	0.57	
Tanytarsini	0.06	8.83 (1)	0.5	
Pediciidae				
<i>Dicranota</i> spp.	0.19	10.78 (2)	0.79	rhp (4)

Species	R ²	FST	Shear Stress	Current preference
Empididae	0.08	10.36	(2)	0.69 ind (4)
Clinocerinae	0.13	10.84	(2)	0.8
Hemerodromiinae	0.04	9.39	(1)	0.57
	0.07	10.49	(2)	0.72
Blephariceridae				
<i>Liponeura spp.</i>	0.81	15.3	(2)	3.59 rhb (3)
Psychodidae	0.13	9.8	(2)	0.61
Simuliidae	0.48	12.31	(1)	1.17 rhb (4)
	0.45	13.47	(2)	1.82
<i>Prosimulium hirtipes</i>	0.19	10.86	(2)	0.81 rhb (3)
<i>Prosimulium rufipes</i>	0.68	15.36	(2)	3.67 rhb (3)
<i>Simulium cryophilum</i>	0.07	8.82	(2)	0.5 rhp (3)
<i>Simulium equinum</i>	0.07	13.35	(2)	1.74 rhp (3)
<i>Simulium monticola</i>	0.68	13.7	(2)	2 rhp (3)
<i>Simulium ornatum</i>	0.32	11.82	(2)	1.04 rhp (3)
<i>Simulium reptans</i>	0.59	14.04	(2)	2.27 rhp (3)
<i>Simulium spp.</i>	0.45	12.91	(2)	1.46
<i>Tipula lateralis</i>	0.02	8.09	(2)	0.41 lib (3)
<i>Tipula montium</i>	0.12	7.37	(2)	0.32 lip (3)
Ephemeroptera				
Amelitidae				
<i>Ameletus inopinatus</i>	0.39	5.1	(2)	0.17 rhp (6)
Baetidae				
<i>Baetis alpinus</i>	0.68	12.76	(2)	1.37 rhp (6)
<i>Baetis fuscatus</i>	0.04	9.98	(1)	0.63 rlp (6)
	0.38	7.98	(2)	0.4
<i>Baetis lutheri</i>	0.51	12.72	(1)	1.35 rhp (6)
<i>Baetis muticus</i>	0.36	10.95	(2)	0.83 rlp (6)
<i>Baetis rhodani</i>	0.18	12.5	(1)	1.23 rhp (6)
	0.47	10.83	(2)	0.8
<i>Baetis spp.</i>	0.2	10.58	(1)	0.72
	0.56	10.35	(2)	0.69
<i>Centroptilum luteolum</i>	0.78	3.83	(2)	0.14 lip (6)
Caenidae				
<i>Caenis beskidensis</i>	0.34	5.78	(2)	0.21 rhp (6)

Species	R ²	FST	Shear Stress	Current preference
<i>Caenis luctuosa</i>	0.42	5.75	(1) 0.21	rlp (6)
	0.03	7.68	(2) 0.36	
<i>Caenis rivulorum</i>	0.03	9.42	(1) 0.57	rhp (6)
	0.04	9.24	(2) 0.55	
<i>Caenis</i> spp.	0.18	7.54	(1) 0.34	
	0.23	8.75	(2) 0.49	
Ephemerellidae				
<i>Ephemerella mucronata</i>	0.21	9.02	(2) 0.53	rlp (6)
<i>Ephemerella notata</i>	0.2	8.38	(2) 0.45	rlp (6)
<i>Ephemerella</i> spp.	0.29	8.1	(2) 0.41	
<i>Serratella ignita</i>	0.07	10.63	(1) 0.73	rlp (6)
Ephemeridae				
<i>Ephemera danica</i>	0.1	6.69	(2) 0.26	rlp (6)
Heptageniidae				
<i>Ecdyonurus venosus</i>	0.18	8.46	(2) 0.46	rlp (6)
<i>Epeorus sylvicola</i>	0.57	13.52	(2) 1.86	rhp (6)
	0.34	7.28	(2) 0.31	
<i>Heptagenia</i> spp.	0.04	11.52	(1) 0.97	
<i>Heptagenia sulphurea</i>	0.24	11.23	(1) 0.9	rlp
<i>Rhithrogena semicolorata</i>	0.22	11.41	(1) 0.94	rhp (6)
	0.43	11.24	(2) 0.9	
<i>Rhithrogena</i> spp.	0.28	12.47	(1) 1.19	
	0.43	11.34	0.92	
Leptophlebiidae				
<i>Habroleptoides confusa</i>	0.1	8.31	(2) 0.44	rlp (6)
<i>Habrophlebia lauta</i>	0.17	7.04	(2) 0.27	lrp (6)
Pothamantidae				
<i>Potamanthus luteus</i>	0.1	9.91	(1) 0.62	rlp (6)
Gastropoda				
Hydrobiidae				
<i>Potamopyrgus antipodarum</i>	0.14	6.19	(1) 0.23	ind (3)
Lymnaeidae				
<i>Radix ovata</i>	0.26	6.48	(2) 0.24	lip (4)
Nertidae				
<i>Theodoxus fluviatilis</i>	0.42	13.05	(1) 1.54	rhp (3)

Species	R ²	FST	Shear Stress	Current preference
Physidae	0.02	9.4	(1)	0.57
Planorbidae				
<i>Ancylus fluviatilis</i>	0.42	13.2	(1)	1.64 rhb (3)
	0.23	7.56	(2)	0.34
Valvatidae				
<i>Valvata</i> spp.	0.02	9.3	(1)	0.56
Hirudinea				
Erpobdellidae				
<i>Erpobdella octoculata</i>	0	8.63	(1)	0.48 ind (3)
Glossiphoniidae	0.09	7.40	(2)	0.32
<i>Glossiphonia complanata</i>	0	8.39	(1)	0.45 ind (3)
	0.33	5.41	(2)	0.19
Heteroptera				
Aphelocheiridae				
<i>Aphelocheirus aestivalis</i>	0.14	8.69	(2)	0.49 rhb (3)
Corixidae				
<i>Micronecta</i> spp.	0.49	3.65	(1)	0.13
Megaloptera				
Sialidae				
<i>Sialis fuliginosa</i>	0.5	5.25	(2)	0.18 rhp (3)
Plecoptera				
Chloroperlidae				
<i>Chloroperla</i> spp.	0.42	4.54	(2)	0.15 rhp (7)
<i>Siphonoperla torrentium</i>	0.13	8.74	(2)	0.49 rhp (7)
Leuctridae				
<i>Leuctra hippopus</i>	0.06	8.32	(2)	0.44 rhp (7)
<i>Leuctra</i> spp.	0.41	12.49	(1)	1.22
	0.14	9.29	(2)	0.56
Nemouridae	0.02	8.73	(2)	0.49
<i>Amphinemura borealis</i>	0.02	10.03	(2)	0.63 ind (7)
<i>Amphinemura</i> spp.	0.05	9.72	(2)	0.6 rhp (4)
<i>Amphinemura sulcicollis</i>	0.05	8.77	(2)	0.5 rhp (7)
<i>Nemoura cambrica</i>	0.06	9.09	(2)	0.54 rhp (7)
<i>Nemoura</i> spp.	0.11	7.86	(2)	0.38 lrh (4)
<i>Protonemura nitida</i>	0.25	9.91	(2)	0.62 ind (7)

Species	R ²	FST	Shear Stress	Current preference
<i>Protonemura spp.</i>	0.24	10.01 (2)	0.63	rhb (4)
Perlidae				
<i>Dinocras cephalotes</i>	0.24	10.67 (2)	0.76	rhp (7)
<i>Perla marginata</i>	0.03	9.54 (2)	0.58	rhp (7)
Perlodidae				
<i>Diura bicaudata</i>	0	7.51 (2)	0.34	rlp (7)
<i>Isoperla obscura</i>	0.17	8.6 (2)	0.48	rhp (7)
<i>Isoperla oxylepis</i>	0.16	9.09 (2)	0.54	rhp (7)
<i>Isoperla rivolorum</i>	0.28	11.26 (2)	0.9	rhp (7)
<i>Isoperla spp.</i>	0.21	9.76 (2)	0.62	rhp (7)
<i>Perlodes microcephalus</i>	0.08	8.08 (2)	0.41	rhp (7)
<i>Perlodes spp.</i>	0.08	8.21 (2)	0.42	rhp (7)
Taeniopterygidae				
<i>Brachyptera risi</i>	0.34	11.2 (2)	0.89	rhp (7)
<i>Brachyptera seticornis</i>	0.65	12.85 (2)	1.42	
Trichoptera				
Brachycentridae				
<i>Micrasema longulum</i>	0.14	12.89 (2)	1.44	rhb (8)
<i>Micrasema minimum</i>	0.04	10.21 (2)	0.65	rhb (8)
Lepidostomatidae				
<i>Lepidostoma hirtum</i>	0.05	8.22 (2)	0.43	lrh (8)
Leptoceridae				
<i>Athripsodes albifrons</i>	0.02	8.36 (1)	0.44	rlp (8)
<i>Athripsodes bilineatus</i>	0.07	11.92 (2)	1.07	rlp (8)
<i>Athripsodes cinereus</i>	0	9.13 (2)	0.54	lrh (8)
<i>Athripsodes spp.</i>	0.28	11.95 (2)	1.08	
<i>Ceraclea dissimilis</i>	0.04	8.05 (1)	0.4	rhp (8)
<i>Ceraclea spp.</i>	0.04	7.66 (1)	0.35	
	0.03	8.28 (2)	0.43	
Glossosomatidae				
<i>Agapetus fuscipes</i>	0.13	11.19 (2)	0.89	rhp (8)
<i>Agapetus spp.</i>	0.09	10.43 (2)	0.69	rhp (8)
<i>Glossosoma boltoni</i>	0.05	9.65 (1)	0.59	rhp (8)
<i>Glossosoma conformis</i>	0.27	8.03 (2)	0.4	rhp (8)
<i>Glossosoma spp.</i>	0.06	9.56 (1)	0.58	rhp (8)

Species	R ²	FST	Shear Stress	Current preference
	0.27	8.02	(2)	0.4
Goeridae	0.03	7.76	(1)	0.37
<i>Goera pilosa</i>	0.06	7.51	(2)	0.34 lip (8)
<i>Silo nigricornis</i>	0.26	6.14	(2)	0.23 rhp (8)
Hydropsychidae				
<i>Hydropsyche angustipennis</i>	0.57	10.96	(2)	0.83 rhp (8)
<i>Hydropsyche contubernalis</i>	0.36	10.2	(1)	0.65 rhp (8)
<i>Hydropsyche dinarica</i>	0.2	11.06	(2)	0.86 rhp (8)
<i>Hydropsyche exocellata</i>	0.24	10.34	(1)	0.66 rhp (8)
<i>Hydropsyche incognita</i>	0.21	11.29	(1)	0.91 rhp (8)
<i>Hydropsyche instabilis</i>	0.29	12.14	(2)	1.13 rhp (8)
<i>Hydropsyche modesta</i>	0.15	9.89	(1)	0.62 rhp (8)
<i>Hydropsyche pellucidula/incognita</i>	0.41	12.7	(2)	1.33 rhp (8)
<i>Hydropsyche siltalai</i>	0.32	13.23	(1)	1.66 rhp (8)
	0.3	12.5	(2)	1.23
<i>Hydropsyche spp.</i>	0.21	10.28	(1)	0.66 rhp (8)
	0.58	12.57	(2)	1.26
Hydroptilidae				
<i>Hydroptila spp.</i>	0.13	6.85	(1)	0.26
<i>Hydroptila tineoides</i>	0.37	13.25	(2)	1.67 lip (8)
Limnephilidae	0.47	5.83	(2)	0.21
<i>Allogamus auricollis</i>	0.37	5.48	(2)	0.19 rhp (8)
<i>Anomalopterygella chauviniana</i>	0.08	8.11	(2)	0.41 rhp (8)
Chaetopterygini	0.49	4.22	(2)	0.15
<i>Chaetopteryx villosa/fusca</i>	0.32	6.21	(2)	0.23 rlp (8)
Drusini	0.06	8.64	(2)	0.48
<i>Drusus annulatus</i>	0.06	5.87	(2)	0.21 rhp (8)
<i>Drusus spp.</i>	0.06	5.87	(2)	0.21 rhp (8)
<i>Ecclisopteryx dalecarlica</i>	0.11	8.02	(2)	0.4 rhp (8)
<i>Ecclisopteryx guttulata</i>	0.18	7.81	(2)	0.37 rhp (8)
<i>Ecclisopteryx spp.</i>	0.19	7.79	(2)	0.37 rhp (8)
Odontoceridae				
<i>Odontocerum albicorne</i>	0.18	8.23	(2)	0.43 rhp (8)
Philopotamidae				
<i>Philopotamus montanus</i>	0.34	12.25	(2)	1.16 lrh (8)

Species	R ²	FST	Shear Stress	Current preference	
Polycentropodidae	0.43	4.47	(1)	0.15	
<i>Polycentropus flavomaculatus</i>	0.3	4.62	(1)	0.16	lrh (8)
	0.14	6.81	(2)	0.26	
Psychomyiidae					
<i>Psychomyia pusilla</i>	0.04	9.41	(1)	0.57	rlp (8)
	0.13	10.54	(2)	0.7	
<i>Tinodes unicolor</i>	0.26	9.36	(2)	0.56	rhp (8)
Rhyacophiliidae					
<i>Rhyacophila dorsalis</i>	0.6	13.09	(2)	1.57	rhb (8)
<i>Rhyacophila nubila</i>	0.47	12.43	(2)	1.2	rhb (8)
<i>Rhyacophila praemorsa</i>	0.2	10.22	(2)	0.65	rhb (8)
<i>Rhyacophila</i> spp.	0.4	11.69	(2)	1.01	rhb (8)
<i>Rhyacophila s. stricto</i> spp.	0.3	11.9	(1)	1.06	
<i>Rhyacophila tristis</i>	0.22	9.28	(2)	0.56	rhb (8)
Sericostomatidae					
<i>Sericostoma personatum</i>	0.02	7.68	(2)	0.36	lrh (8)
<i>Sericostoma</i> spp.	0.08	8.39	(2)	0.44	lrh (8)
Uenoidae					
<i>Thremma gallicium</i>	0.11	6.23	(2)	0.23	rhp (8)
Turbellaria					
Dendrocoelidae					
<i>Dendrocoelum lacteum</i>	0.01	7.57	(1)	0.34	ind (3)
Dugesiiidae					
<i>Dugesia polychroa-lugubris</i>	0.13	12.73	(1)	1.35	lip (3)
<i>Dugesia tigrina</i>	0.15	10.69	(1)	0.77	lrh (3)
Planariidae					
<i>Polycelis nigra-tenuis</i>	0.14	5.69	(1)	0.2	lrh (3)

Table 9 Critical shear stress thresholds (N /m²) detaching and dislodging benthic invertebrates; CWD= coarse woody debris.

Species	Habitat	Critical shear stress (N /m ²)	Study
Amphipoda			
<i>Dikerogammarus villosus</i>	Sand	0.48	Gabel et al. (2012)
	Stones	1.51	Gabel et al. (2012)
	CWD	0.94	Gabel et al. (2012)
	Reed	0.42	Gabel et al. (2012)
	Roots	>1.7	Gabel et al. (2012)
<i>Gammarus pulex</i>	...	3.1	Borchardt (1993)
<i>Gammarus roeselii</i>	Sand	0.42	Gabel et al. (2012)
	Stones	0.49	Gabel et al. (2012)
	CWD	0.62	Gabel et al. (2012)
	Reed	0.57	Gabel et al. (2012)
	Roots	>1.7	Gabel et al. (2012)
Coleoptera			
<i>Laccophilus hyalinus</i>	Sand	0.23	Gabel et al. (2012)
	Stones	0.23	Gabel et al. (2012)
	CWD	0.44	Gabel et al. (2012)
	Reed	0.41	Gabel et al. (2012)
	Roots	0.99	Gabel et al. (2012)
Diptera			
<i>Athericidae gen.sp.</i>	Gravel/Cobble	0.42	Hauer et al. (2012)
Ephemeroptera			
<i>Baetis sp.</i>	Gravel/Cobble	0.26	Hauer et al. (2012)
	Gravel	9	Gibbins et al. (2010)
<i>Caenis sp.</i>	Gravel	9	Gibbins et al. (2010)
<i>Ecdyonurus sp.</i>	Gravel	9	Gibbins et al. (2010)
<i>Epeorus assimilis</i>	Gravel/Cobble	0.33	Hauer et al. (2012)
<i>Heptagenia sp.</i>	Sand	5.18	Schnauder et al. (2010)
<i>Rhithrogena sp.</i>	Gravel/Cobble	0.37	Hauer et al. (2012)
<i>Serratella ignita</i>	...	1.1	Borchardt (1993)
Gastropoda			
<i>Bithynia tentaculata</i>	Sand	0.44	Schnauder et al. (2010)
	Sand	0.57	Gabel et al. (2012)
	Stones	0.55	Gabel et al. (2012)

Species	Habitat	Critical shear stress (N /m ²)	Study
<i>Viviparus viviparus</i>	CWD	0.48	Gabel et al. (2012)
	Reed	0.86	Gabel et al. (2012)
	Roots	1.22	Gabel et al. (2012)
	Sand	2.40	Schnauder et al. (2010)
Hirudinea			
<i>Piscicola geometra</i>	Sand	2.50	Schnauder et al. (2010)
Megaloptera			
<i>Sialis lutaria</i>	Sand	0.1	Schnauder et al. (2010)
Odonata			
<i>Aeshna cyanea</i>	Sand	1.12	Blanckaert et al. (2012)
<i>Calopteryx splendens</i>	Sand	2.40	Schnauder et al. (2010)
	Sand	0.13	Gabel et al. (2012)
	Stones	0.13	Gabel et al. (2012)
	CWD	0.36	Gabel et al. (2012)
	Reed	0.84	Gabel et al. (2012)
	Roots	>1.7	Gabel et al. (2012)
<i>Coenagrionidae sp.</i>	Sand	5.78	Schnauder et al. (2010)
<i>Cordulia aenea</i>	Sand	1.94	Schnauder et al. (2010)
<i>Gomphus vulgatissimus</i>	Sand	0.23	Schnauder et al. (2010)
<i>Somatochlora flavomaculata</i>	Sand	0.87	Blanckaert et al. (2012)
Plecoptera			
<i>Perla sp.</i>	Gravel/Cobble	1.75	Hauer et al. (2012)
Trichoptera			
<i>Allogamus auricollis</i>	Gravel/Cobble	3.04	Hauer et al. (2012)
<i>Anabolia nervosa</i>	Sand	0.20	Schnauder et al. (2010)
<i>Hydropsyche sp.</i>	Gravel/Cobble	0.48	Hauer et al. (2012);
	Sand	>5.78	Schnauder et al. (2010)
<i>Rhyacophila sp.</i>	Gravel/Cobble	0.66	Hauer et al. (2012)

Table 10 Summary of reported physical spawning sites properties of gravel spawning lamprey and fish species (spawner type: OSP= open substrate spawner, BH= brood hider, GUA= guarder; gravel diameter: d_m = mean, d_{50} = median, d_g = geometric mean).

Fish species		Spawner type	Spawning gravel diameter (mm)					Fredle Index	% fines <0.85 mm	Fish length Lt (cm)	Water depth (m)			Egg depth (m)	Flow velocity (m/s)			Source
			min	max	d_m	d_{50}	d_g				min	max	mean		min	max	mean	
Allis shad	<i>Alosa alosa</i>	OSP	30	160	75				48								1	
Allis shad	<i>Alosa alosa</i>	OSP	20	200					48								1	
Allis shad	<i>Alosa alosa</i>	OSP	30	80	70				48								1	
Allis shad	<i>Alosa alosa</i>	OSP	20	130	50				48								1	
Allis shad	<i>Alosa alosa</i>	OSP	70						40	0.5	1.5			1			4	
Asp	<i>Aspius aspius</i>	OSP	20	120	50.6				62					0.13	0.58	0.38	57	
Atlantic salmon	<i>Salmo salar</i>	BH	8	64					71	0.15	0.91	0.3-0.45	0.22	0.2	0.81		16	
Atlantic salmon	<i>Salmo salar</i>	BH			92				73	0.2	1.2	0.49	0.18	0.01	0.8	0.39	27	
Atlantic salmon	<i>Salmo salar</i>	BH				36.7		4.6	76								30	
Atlantic salmon	<i>Salmo salar</i>	BH				33.9		10.3	76								30	
Atlantic salmon	<i>Salmo salar</i>	BH				50.4		27.2	76								30	
Atlantic salmon	<i>Salmo salar</i>	BH				11.45	4.92	23.41	75	0.25	0.3	0.26		0.5	0.65	0.52	52	
Atlantic salmon	<i>Salmo salar</i>	BH				20.73	9.98	12.34	75	0.15	0.2	0.24		0.35	0.65	0.54	52	
Atlantic sturgeon	<i>Acipenser sturion</i>	OSP	30	300					178	1	12			0.4	2		19	
Barbel	<i>Barbus barbus</i>	OSP	20	50		50			51	0.14	0.22			0.35	0.49		15	
Barbel	<i>Barbus barbus</i>	OSP	10	30					51	0.25	0.4			0.21	0.6		17	

Fish species	Spawner	Spawning gravel diameter (mm)	Fredle	% fines	Fish	Water depth (m)	Egg	Flow velocity (m/s)	Source											
										type	Index			length	depth					
											min	max	d _m		d ₅₀	d _g	<0.85 mm	Lt (cm)	min	max
Barbel	<i>Barbus barbus</i>	OSP	20	250																
Barbel	<i>Barbus barbus</i>	OSP	2	60																
Brook lamprey	<i>Lampetra planeri</i>	BH	11	30	21															
Brook trout	<i>Salvelinus fontinalis</i>	BH	0.25	63		9.2	5.7		23.7	17		0.24			0.03	0.42	0.18			55
Brown trout	<i>Salmo trutta</i>	BH	4	64				3.4-5.4	6.5	35										5
Brown trout	<i>Salmo trutta</i>	BH	4	30						32	10	50			0.15	0.6				21
Brown trout	<i>Salmo trutta</i>	BH	7	75						30	0.06	0.3	0.16		0.24	0.37				22
Brown trout	<i>Salmo trutta</i>	BH			81					32	0.1	0.7	0.5	0.12	0.01	0.6	0.27			27
Brown trout	<i>Salmo trutta</i>	BH	10	70						32	0.1	0.5			0.3	0.5				31
Brown trout	<i>Salmo trutta</i>	BH	10	30						32	0.15	0.28			0.12	0.25				36
Brown trout	<i>Salmo trutta</i>	BH				27			8.5	32										39
Brown trout	<i>Salmo trutta</i>	BH				6			34.5	32										39
Brown trout	<i>Salmo trutta</i>	BH	18	32						32										42
Brown trout	<i>Salmo trutta</i>	BH			64.6				7.3	29			0.15	0.08	0.3	0.4	0.39			43
Brown trout	<i>Salmo trutta</i>	BH	16	130				4.9	7.1	38			0.5	0.1			0.15			44
Brown trout	<i>Salmo trutta</i>	BH	16	130				7.1	7.5	38			0.65	0.1			0.34			44
Brown trout	<i>Salmo trutta</i>	BH	6	76						32	0.24	0.45			0.4	0.7				47
Brown trout	<i>Salmo trutta</i>	BH	10	70						32	0.12	0.91	0.32		0.15	0.9	0.44			47

Fish species		Spawner type	Spawning gravel diameter (mm)					Fredle Index	% fines <0.85 mm	Fish length Lt (cm)	Water depth (m)			Egg depth (m)	Flow velocity (m/s)			Source
			min	max	d _m	d ₅₀	d _g				min	max	mean		min	max	mean	
Brown trout	<i>Salmo trutta</i>	BH	5	28	14				43	0.08	0.82	0.31		0.15	0.75	0.39	51	
Brown trout	<i>Salmo trutta</i>	BH	1	63		9.9	6.9	17.1	25			0.26		0.11	0.8	0.46	55	
Brown trout (lake form)	<i>Salmo trutta</i>	BH	16	64					64	18	50	32.17		0.28	0.85	0.55	14	
Bullhead	<i>Cottus gobio</i>	GUA	20	200					10	0.2	0.4			0.1	0.8	0.5	8	
Burbot	<i>Lota lota</i>	OSP	25	80					58.5								40	
Chub	<i>Leuciscus cephalus</i>	OSP	2	80	39				35	0.05	1.28				0.05		2	
Chub	<i>Leuciscus cephalus</i>	OSP	50	250					46	0.1	1			0.15	0.35		18	
Chub	<i>Leuciscus cephalus</i>	OSP	5						40					0.2	0.5		35	
Dace	<i>Leuciscus leuciscus</i>	OSP	30	250					20	0.15	0.4						35	
Danube salmon	<i>Hucho hucho</i>	BH	10	50					70	0.2	0.8			0.2	0.7		28	
Danube salmon	<i>Hucho hucho</i>	BH	1	60					70	0.3	0.6			0.2			46	
Danube salmon	<i>Hucho hucho</i>	BH	16	63					70	0.2	0.63			0.3	0.35		49	
Danube salmon	<i>Hucho hucho</i>	BH	16	63					70	0.2	0.6				0.3		48	
Danubian brook lamprey	<i>Eudontomyzon vladykovi</i>	BH	0.2	20	2				20			0.5		0.02	0.2		32	
Grayling	<i>Thymallus thymallus</i>	BH	2	64					40	0.2	0.5			0.04	0.5	0.75	3	
Grayling	<i>Thymallus thymallus</i>	BH	17	64					32	0.26	0.3			0.03	0.4	0.8	7	
Grayling	<i>Thymallus thymallus</i>	BH	2	20					40	0.3	0.55	0.43		0.07	0.23	0.57	0.39	20
Grayling	<i>Thymallus thymallus</i>	BH	5	60					40	0.2	0.5			0.05	0.2	0.5	24	

Fish species		Spawner type	Spawning gravel diameter (mm)					Fredle Index	% fines <0.85 mm	Fish length Lt (cm)	Water depth (m)			Egg depth (m)	Flow velocity (m/s)			Source
			min	max	d _m	d ₅₀	d _g				min	max	mean		min	max	mean	
			Grayling	<i>Thymallus thymallus</i>	BH	8	64									40	0.1	
Grayling	<i>Thymallus thymallus</i>	BH	20	63	35.4		11.97	3.3	41	0.25	0.64	0.41	0.36	0.88	0.61	29		
Grayling	<i>Thymallus thymallus</i>	BH	16	64					40	0.13	0.57	0.27	0.13	0.87	0.37	50		
Gudgeon	<i>Gobio gobio</i>	OSP	3	30					10				0.1	0.8		15		
Minnow	<i>Phoxinus phoxinus</i>	OSP	20	30					8.5				0.2	0.3		9		
Nase	<i>Chondrostoma nasus</i>	OSP	10	80	38				48.5	0.15	0.3		0.5	0.7		34		
Nase	<i>Chondrostoma nasus</i>	OSP	20	160	67				50	0.3	0.4		0.65	1.1		34		
Nase	<i>Chondrostoma nasus</i>	OSP	10	100					45				0.7	0.9		35		
Nase	<i>Chondrostoma nasus</i>	OSP	20	200					40	0.16	0.83	0.34	0.2	0.97	0.67	38		
Nase	<i>Chondrostoma nasus</i>	OSP	20	63					45	0.15	0.3		0.6	0.8		37		
Nase	<i>Chondrostoma nasus</i>	OSP	10	70	34				45							58		
Nase	<i>Chondrostoma nasus</i>	OSP	20	180	71				45							58		
Nase	<i>Chondrostoma nasus</i>	OSP	10	170	67				45							58		
Nase	<i>Chondrostoma nasus</i>	OSP	27	67					48	0.1	0.3		0.7	1.1		59		
Rainbow trout	<i>Oncorhynchus mykiss</i>	BH			23.5	14.7		6.3	75							26		
Rainbow trout	<i>Oncorhynchus mykiss</i>	BH			33.4	24.5		1.5	40							33		
Rainbow trout	<i>Oncorhynchus mykiss</i>	BH			10.5	5.6		6.8	45							33		
Rainbow trout	<i>Oncorhynchus mykiss</i>	BH			20	12.4		7	30							45		

Fish species		Spawner type	Spawning gravel diameter (mm)					Fredle Index	% fines <0.85 mm	Fish length Lt (cm)	Water depth (m)			Egg depth (m)	Flow velocity (m/s)			Source
			min	max	d _m	d ₅₀	d _g				min	max	mean		min	max	mean	
Rainbow trout	<i>Oncorhynchus mykiss</i>	BH			12.5	8.3		11.1	44								54	
Savetta	<i>Chondrostoma soetta</i>	OSP	2	60	16				37	0.5							34	
Sea lamprey	<i>Petromyzon marinus</i>	BH	10	50					85	0.4	0.6		1	2			25	
Sea lamprey	<i>Petromyzon marinus</i>	BH	1	16	5.66			11.9	88.2	0.1	0.7						53	
Sea trout	<i>Salmo trutta</i>	BH	1	64	18	8.5	3.54		68	0.25	0.5	0.35	0.37	0.91	0.64		41	
Sea trout	<i>Salmo trutta</i>	BH	1	64	24.9	16.2	8.13		68	0.26	0.42	0.32	0.4	0.86	0.54		41	
Smelt	<i>Osmerus eperlanus</i>	OSP	1	200					9	0.3	3		0	0.3	1		6	
Smelt	<i>Osmerus eperlanus</i>	OSP	6	60					10	0.07	0.1		0				13	
Soufie	<i>Leuciscus souffia</i>	OSP	20	80					16			0.2	0.15	0.37			10	
Soufie	<i>Leuciscus souffia</i>	OSP	10	30					12				0.15	0.5			12	
Spirilin	<i>Alburnoides bipunctatus</i>	OSP	20	150					8.5				0.4	0.4			10	
Spirilin	<i>Alburnoides bipunctatus</i>	OSP	4	80					9				0.34	0.54			12	
Spirilin	<i>Alburnoides bipunctatus</i>	OSP	30	250					10				0.2	0.5			35	
Toxostome	<i>Chondrostoma toxostoma</i>	OSP	10	100	35				21	0.05	0.4				0.5		34	
Toxostome	<i>Chondrostoma toxostoma</i>	OSP	10	100					22	0.05	0.4				0.5		59	
Twaite shad	<i>Alosa fallax</i>	OSP	20	120	70				35								1	
Whitefish	<i>Coregonus maraena</i>	OSP	0.6	10					40	1	3		0.3	0.5			56	

Sources: 1 Aprahamian et al. (2003), 2 Arlinghaus & Wolter (2003), 3 Baars et al. (2001), 4 Bartl & Troschel (1995), 5 Beard & Carline (1991), 6 Belyanina (1969), 7 Blackman (2002), 8 Bless (1983), 9 Bless (1992), 10 Bless (1996), 11 Bohl (1995), 12 Bohl et al. (2004), 13 Bruce (1975), 14 Caviezel



(2006), 15 Cowx et al. (2004), 16 Crisp (1996), 17 Ebel (2002), 18 Fredrich et al. (2003), 19 Gessner & Bartel (2000), 20 Gönczi (1989), 21 Gortázar et al. (2012), 22 Grost et al. (1990), 23 Guthruf (1996), 24 Guthruf & Peter (1992), 25 Hardisty (1986), 26 Hartman & Galbraith (1970, cited in Kondolf 2000), 27 Heggberget et al. (1988), 28 Holzer (2000), 29 Hübner (2003), 30 Julien & Bergeron (2006), 31 Jungwirth et al. (2003), 32 Kappus et al. (1994), 33 Kondolf et al. (1989), 34 Maier et al. (1995), 35 Mann (1996), 36 Mayo et al. (1995, cited by Gortázar et al. 2012), 37 Melcher (1999), 38 Melcher & Schmutz (2010), 39 Milan et al. (2000), 40 Neufeld et al. (2011), 41 Nika et al. (2011), 42 Olsson & Persson (1986), 43 Ottaway et al. (1981), 44 Pender & Kwak (2002), 45 Platts et al. (1979, cited in Kondolf 2000), 46 Prawochensky & Kolder (1968), 47 Raleigh et al. (1986), 48 Schulz (1989), 49 Schulz & Piery (1982), 50 Sempeski & Gaudin (1995), 51 Shirvell & Dungey (1983), 52 Soulsby et al. (2001), 53 Sousa et al. (2012), 54 Spoon (1985, cited in Kondolf 2000), 55 Witzel & MacCrimmon (1983), 56 Wolter (unpublished), 57 Wolter et al. (2005), 58 Zbinden & Hefti (2000), 59 Zbinden & Maier (1996)

Table 11 Characterisation of European lamprey and fish species by their probability of occurrence in the river regions ER= epirhithral, MR= metarhithral, HR= hyporhithral, EP= epipotamal, MP= metapotamal, HP= hypopotamal, with the resulting Fish Region Index (FRI) and variance (S²FRI). Recent taxonomic improvements are added (Freyhof).

Species name (EFI+)	Species name (Freyhof)	ER 3	MR 4	HR 5	EP 6	MP 7	HP 8	FRI	S ² FRI
Abramis ballerus	Ballerus ballerus				2	7	3	7.08	0.45
Abramis bjoerkna	Blicca bjoerkna				3	6	3	7.00	0.55
Abramis brama	Abramis brama				3	6	3	7.00	0.55
Abramis sapa	Ballerus sapa				4	7	1	6.75	0.39
Achondrostoma arcasii	Achondrostoma arcasii			2	10			5.83	0.15
Achondrostoma occidentale	Achondrostoma occidentale			2	10			5.83	0.15
Achondrostoma oligolepis	Achondrostoma oligolepis			2	8	2		6.00	0.36
Acipenser baeri	Acipenser baeri			1	3	4	4	6.92	0.99
Acipenser gueldenstaedtii	Acipenser gueldenstaedtii				1	5	6	7.42	0.45
Acipenser naccarii	Acipenser naccarii				2	5	5	7.25	0.57
Acipenser nudiventris	Acipenser nudiventris				2	6	4	7.17	0.52
Acipenser oxyrinchus	Acipenser oxyrinchus				1	5	6	7.42	0.45
Acipenser ruthenus	Acipenser ruthenus				3	6	3	7.00	0.55
Acipenser stellatus	Acipenser stellatus				1	5	6	7.42	0.45
Acipenser sturio	Acipenser sturio				1	5	6	7.42	0.45
Alburnoides bipunctatus	Alburnoides bipunctatus		1	5	6			5.42	0.45
Alburnus alburnus	Alburnus alburnus			1	4	6	1	6.58	0.63
Alosa alosa	Alosa alosa				4	4	4	7.00	0.73
Alosa fallax	Alosa fallax					3	9	7.75	0.20
Alosa immaculata	Alosa immaculata					4	8	7.67	0.24
Alosa tanaica	Alosa tanaica				1	4	7	7.50	0.45
Ameiurus melas	Ameiurus melas				5	7		6.58	0.27
Ameiurus nebulosus	Ameiurus nebulosus				5	7		6.58	0.27
Anaocypris hispanica	Anaocypris hispanica			3	9			5.75	0.20
Anguilla anguilla	Anguilla anguilla		1	1	3	3	4	6.67	1.70
Aspius aspius	Leuciscus aspius				4	7	1	6.75	0.39
Atherina boyeri	Atherina boyeri					2	10	7.83	0.15
Barbatula barbatula	Barbatula barbatula		3	4	4	1		5.25	0.93
Barbus carpaticus	Barbus carpaticus		2	8	2			5.00	0.36
Barbus barbus	Barbus barbus			2	7	3		6.08	0.45
Barbus bocagei	Luciobarbus bocagei			1	4	6	1	6.58	0.63
Barbus comizo	Luciobarbus comizo			2	7	3		6.08	0.45
Barbus microcephalus	Luciobarbus microcephalus			2	4	5	1	6.42	0.81
Barbus petenyi	Barbus petenyi		2	8	2			5.00	0.36
Barbus sclateri	Luciobarbus sclateri			2	5	4	1	6.33	0.79
Barbus steindachneri	Luciobarbus steindachneri			2	5	4	1	6.33	0.79
Benthophiloides brauneri	Benthophiloides brauneri					7	5	7.42	0.27
Benthophilus stellatus	Benthophilus stellatus					9	3	7.25	0.20
Carassius auratus	Carassius auratus				3	9		6.75	0.20
Carassius carassius	Carassius carassius				2	9	1	6.92	0.27
Carassius gibelio	Carassius gibelio			1	4	5	2	6.67	0.79
Chalcalburnus chalcoides	Alburnus chalcoides			5	7			5.58	0.27
Chondrostoma nasus	Chondrostoma nasus		1	3	7	1		5.67	0.61
Chondrostoma toxostoma	Parachondrostoma toxostoma		1	3	8			5.58	0.45
Clupeonella cultriventris	Clupeonella cultriventris					3	9	7.75	0.20
Cobitis calderoni	Cobitis calderoni		2	5	5			5.25	0.57
Cobitis elongata	Cobitis elongata			4	6	2		5.83	0.52
Cobitis elongatoides	Cobitis elongatoides		1	2	3	5	1	6.25	1.30
Cobitis paludica	Cobitis paludica		1	5	3	3		5.67	0.97
Cobitis taenia	Cobitis taenia			1	5	5	1	6.50	0.64
Cobitis tanaitica	Cobitis tanaitica					5	7	7.58	0.27
Coregonus maraena	Coregonus maraena				1	6	5	7.33	0.42

Species name (EFI+)	Species name (Freyhof)	ER 3	MR 4	HR 5	EP 6	MP 7	HP 8	FRI	S ² FRI
Coregonus oxyrinchus	Coregonus oxyrinchus				1	7	4	7.25	0.39
Cottus gobio	Cottus gobio	4	4	2	2			4.17	1.24
Cottus poecilopus	Cottus poecilopus	2	5	3	2			4.42	0.99
Ctenopharyngodon idella	Ctenopharyngodon idella					10	2	7.17	0.15
Cyprinus carpio	Cyprinus carpio				2	8	2	7.00	0.36
Dicentrarchus labrax	Dicentrarchus labrax					2	10	7.83	0.15
Esox lucius	Esox lucius			2	3	5	2	6.58	0.99
Eudontomyzon danfordi	Eudontomyzon danfordi	1	5	5	1			4.50	0.64
Eudontomyzon mariae	Eudontomyzon mariae		3	4	3	2		5.33	1.15
Eudontomyzon vladykovi	Eudontomyzon vladykovi		2	7	3			5.08	0.45
Gambusia holbrooki	Gambusia holbrooki			2	3	4	3	6.67	1.15
Gasterosteus aculeatus	Gasterosteus aculeatus			1	2	3	6	7.17	1.06
Gasterosteus gymnurus	Gasterosteus gymnurus				2	8	2	7.00	0.36
Gobio albipinnatus	Romanogobio albipinnatus			1	5	6		6.42	0.45
Gobio gobio	Gobio gobio		1	4	4	2	1	5.83	1.24
Gobio kesslerii	Romanogobio kesslerii			1	4	7		6.50	0.45
Gobio lozanoi	Gobio lozanoi			2	6	4		6.17	0.52
Gymnocephalus baloni	Gymnocephalus baloni				3	7	2	6.92	0.45
Gymnocephalus cernuus	Gymnocephalus cernua				1	5	6	7.42	0.45
Gymnocephalus schraetser	Gymnocephalus schraetser				5	5	2	6.75	0.57
Hucho hucho	Hucho hucho			5	7			5.58	0.27
Huso huso	Huso huso				3	4	5	7.17	0.70
Hypophthalmichthys molitrix	Hypophthalmichthys molitrix				1	9	2	7.08	0.27
Hypophthalmichthys nobilis	Hypophthalmichthys nobilis				1	9	2	7.08	0.27
Iberochondrostoma almaçai	Iberochondrostoma almaçai			2	10			5.83	0.15
Iberochondrostoma lemmingii	Iberochondrostoma lemmingii			2	8	2		6.00	0.36
Iberochondrostoma lusitanicum	Iberochondrostoma lusitanicum			2	8	1		5.42	0.51
Knipowitschia cameliae	Knipowitschia cameliae						12	8.00	0.00
Knipowitschia caucasica	Knipowitschia caucasica					7	5	7.42	0.27
Knipowitschia longecaudata	Knipowitschia longecaudata					1	11	7.92	0.08
Lampetra fluviatilis	Lampetra fluviatilis		2	6	4			5.17	0.52
Lampetra planeri	Lampetra planeri		6	5	1			4.58	0.45
Lepomis gibbosus	Lepomis gibbosus				3	8	1	6.83	0.33
Leucaspius delineatus	Leucaspius delineatus				3	8	1	6.83	0.33
Leuciscus borysthenicus	Petroleuciscus borysthenicus				4	7	1	6.75	0.39
Leuciscus cephalus	Squalius cephalus		1	4	4	2	1	5.83	1.24
Leuciscus idus	Leuciscus idus				4	6	2	6.83	0.52
Leuciscus leuciscus	Leuciscus leuciscus		1	4	4	3		5.75	0.93
Leuciscus souffia	Telestes souffia			7	5			5.42	0.27
Liza aurata	Chelon aurata						12	8.00	0.00
Liza ramada	Chelon ramada						12	8.00	0.00
Liza saliens	Chelon saliens						12	8.00	0.00
Lota lota	Lota lota		1	2	3	4	2	6.33	1.52
Mesogobius batrachocephalus	Mesogobius batrachocephalus						12	8.00	0.00
Micropterus salmoides	Micropterus salmoides			1	5	6		6.42	0.45
Misgurnus fossilis	Misgurnus fossilis				2	8	2	7.00	0.36
Mugil cephalus	Mugil cephalus						12	8.00	0.00
Mugil soiuy	Liza haematocheilus						12	8.00	0.00
Mylopharyngodon piceus	Mylopharyngodon piceus					7	5	7.42	0.27
Neogobius cephalargoides	Ponticola eurycephalus					8	4	7.33	0.24
Neogobius fluviatilis	Neogobius fluviatilis				2	5	5	7.25	0.57
Neogobius gymnotrachelus	Babka gymnotrachelus				2	5	5	7.25	0.57
Neogobius kessleri	Ponticola kessleri				3	6	3	7.00	0.55
Neogobius melanostomus	Neogobius melanostomus				2	5	5	7.25	0.57
Neogobius syrman	Ponticola syrman					2	10	7.83	0.15
Oncorhynchus mykiss	Oncorhynchus mykiss	4	4	4				4.00	0.73
Osmerus eperlanus	Osmerus eperlanus				1	5	6	7.42	0.45

Species name (EFI+)	Species name (Freyhof)	ER 3	MR 4	HR 5	EP 6	MP 7	HP 8	FRI	S ² FRI
Pelecus cultratus	Pelecus cultratus				2	4	6	7.33	0.61
Perca fluviatilis	Perca fluviatilis			1	3	4	4	6.92	0.99
Percarina demidoffi	Percarina demidoffi					4	8	7.67	0.24
Perccottus glenii	Perccottus glenii				3	8	1	6.83	0.33
Petromyzon marinus	Petromyzon marinus			4	7	1		5.75	0.39
Phoxinus phoxinus	Phoxinus phoxinus	1	4	5	2			4.67	0.79
Platichthys flesus	Platichthys flesus				1	4	7	7.50	0.45
Polyodon spathula	Polyodon spathula				1	10	1	7.00	0.18
Pomatoschistus microps	Pomatoschistus microps						12	8.00	0.00
Proterorhinus marmoratus	Proterorhinus semilunaris				3	5	4	7.08	0.63
Pseudochondrostoma duriense	Pseudochondrostoma duriense			3	5	4		6.08	0.63
Pseudochondrostoma polylepis	Pseudochondrostoma polylepis			3	5	4		6.08	0.63
Pseudochondrostoma willkommii	Pseudochondrostoma willkommii			3	5	4		6.08	0.63
Pseudorasbora parva	Pseudorasbora parva			1	4	6	1	6.58	0.63
Pungitius platygaster	Pungitius platygaster				2	7	3	7.08	0.45
Pungitius pungitius	Pungitius pungitius				2	6	4	7.17	0.52
Rhodeus amarus	Rhodeus amarus				6	6		6.50	0.27
Romanichthys valsanicola	Romanichthys valsanicola			5	7			5.58	0.27
Romanogobio antipai	Romanogobio antipai			1	4	4	3	6.75	0.93
Romanogobio belingi	Romanogobio belingi				5	7		6.58	0.27
Romanogobio uranoscopus	Romanogobio uranoscopus			3	7	2		5.92	0.45
Romanogobio vladkovi	Romanogobio vladkovi			2	4	6		6.33	0.61
Rutilus frisii	Rutilus frisii			2	8	2		6.00	0.36
Rutilus heckelii	Rutilus heckelii			3	5	4		6.08	0.63
Rutilus pigus	Rutilus pigus			1	7	4		6.25	0.39
Rutilus rutilus	Rutilus rutilus			1	3	5	3	6.83	0.88
Sabanejewia aurata	Sabanejewia baltica			3	6	3		6.00	0.55
Sabanejewia balcanica	Sabanejewia balcanica			2	4	5	1	6.42	0.81
Sabanejewia bulgarica	Sabanejewia bulgarica			2	6	3	1	6.25	0.75
Sabanejewia romanica	Sabanejewia romanica		1	7	4			5.25	0.39
Salmo labrax	Salmo labrax					2	10	7.83	0.15
Salmo salar	Salmo salar		3	6	3			5.00	0.55
Salmo trutta fario	Salmo trutta	5	5	2				3.75	0.57
Salmo trutta lacustris	Salmo trutta		8	4				4.33	0.24
Salmo trutta trutta	Salmo trutta		3	6	3			5.00	0.55
Salvelinus fontinalis	Salvelinus fontinalis	6	6					3.50	0.27
Sander lucioperca	Sander lucioperca				2	5	5	7.25	0.57
Sander volgensis	Sander volgensis				2	5	5	7.25	0.57
Scardinius erythrophthalmus	Scardinius erythrophthalmus				3	7	2	6.92	0.45
Scardinius racovitzai	Scardinius racovitzai				3	9		6.75	0.20
Silurus glanis	Silurus glanis				2	8	2	7.00	0.36
Squalius alburnoides	Iberocypris alburnoides			3	7	2		5.92	0.45
Squalius aradensis	Squalius aradensis			1	10	1		6.00	0.18
Squalius carolitertii	Squalius carolitertii		1	4	6	1		5.58	0.63
Squalius pyrenaicus	Squalius pyrenaicus		1	4	6	1		5.58	0.63
Squalius torgalensis	Squalius torgalensis		1	4	6	1		5.58	0.63
Syngnathus abaster	Syngnathus abaster					6	6	7.50	0.27
Thymallus thymallus	Thymallus thymallus		3	7	2			4.92	0.45
Tinca tinca	Tinca tinca				3	7	2	6.92	0.45
Umbra krameri	Umbra krameri				1	10	1	7.00	0.18
Vimba vimba	Vimba vimba			1	4	5	2	6.67	0.79
Zingel streber	Zingel streber			2	7	3		6.08	0.45
Zingel zingel	Zingel zingel				8	4		6.33	0.24
Zosterisessor ophiocephalus	Zosterisessor ophiocephalus						12	8.00	0.00