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REstoring rivers FOR effective catchment Management

Deliverable D2.2 part 2

Title Influence of Natural Hydromorphological Dynamics on Biota and Ecosystem Function, Part 2 (Chapters 4 to 6 of 6)

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Summary

Background and Introduction to Deliverable 2.2. Work Package 2 of REFORM focuses on hydromorphological and ecological processes and interactions within river systems with a particular emphasis on naturally functioning systems. It provides a context for research on the impacts of hydromorphological changes in Work Package 3 and for assessments of the effects of river restoration in Work Package 4. Deliverable 2.1 of work package 2 proposes a hierarchical framework to support river managers in exploring the causes of river management problems and devising sustainable solutions. Deliverable 2.2 builds on the framework devised in Deliverable 2.1 by exploring published research and available data sets to more formally encompass the biota.

This report (Part 2 of Deliverable 2.2) extends the research focus beyond vegetation and, within the context of the multi-scale framework, considers interactions between hydromorphology and biota more generally, including specific considerations of macroinvertebrates and fish (Chapter 4), and the role of floods and droughts as biota-shaping phenomena (Chapter 5). Lastly, part 2 presents conclusions from the whole of Deliverable 2.2 (Chapter 6).

<u>Summary of Deliverable 2.2 Part 2.</u>

<u>Research Objective.</u>

The research developed in this report builds upon the Hierarchical Framework developed in Deliverable 2.1 to investigate links between ecology and hydromorphology at multiple scales considering its relevance for the better understanding of river fauna (macroinvertebrates and fish) functioning as well as incorporating extreme hydrological events as biota-shaping phenomena.

<u>Methods and Results.</u>

We have chosen the literature reviews in order to combine knowledge from multiple studies in a given topic, and to summarize the latest evidence. In sections 4.1, 4.2 and 5.1 we adopt a narrative form. In setions 5.2 we undertake a systematic review, using an explicit method to perform a comprehensive literature search and critical appraisal of the individual studies. As a result we are able to prove the usefulness and research gaps when employing the multi-scale framework as a basic tool for developing understanding of river ecosystem organization.

<u>Conclusions and Recommendations.</u>

The evidence extracted from the literature in relation to fish and macroinvertebrates in Chapter 4 demonstrates that their composition and functioning corresponds to the Hierarchical Framework of spatial scales. However, it is clear that some levels of this hierarchical structure are more relevant than others for understanding the mechanisms of biological response to environmental change. It is also evident from the literature review and data analysis presented in Chapter 5 that both floods and droughts are phenomena that shape the structure and composition of aquatic communities. To some extent the impact of these events is moderated by the morphological characteristics of the affected river channels and their floodplains, particularly reflecting the importance of the higher complexity of naturally-functioning rivers, especially multi-thread and floodplain river systems. There is a general pattern of biological response indicating that both types of events lead to changes in aquatic community structure, limiting the

organisms that are less adapted to the disturbance and promoting those with better adaptations. However, responses to events of different type, magnitude, intensity and duration are highly variable.

Looking for the research gaps, we have found that the use of the Hierarchical Framework of spatial scales, linking macrobenthic structure and fish behaviour with functional Hydromorphology, is an important tool for understanding river ecosystem organization. However, a fuller understanding could be developed if purpose-specific data sets were collected, which incorporate the full range of scales and hydromorphological phenomena into investigations of the presence and dynamics of the fauna. A particularly profitable endeavour would be to align typical hydrological, hydraulic and geomorphic units along typical river types to analyse their correspondence with the fish-based river typology (FRI). Moreover, the literature review (section 5.1) and the meta-analysis (section 5.2) suggest that a key research area remains in developing a more robust and deeper understanding of the mechanisms of biological responses to environmental changes and extreme events across different, specific, time and space scales.

In terms of practical recommendations we have shown how interactions between plants and hydromorphology take on different characteristics in different biogeographical settings, leading to different spatial distributions and temporal dynamics. These long-overlooked dynamics need serious research and management attention. Riparian vegetation needs to be more formally incorporated into the Water Framework Directive and as a fundamental component of river management and restoration design.

We have also proved that moving beyond the reach scale to consider the broader spatial and temporal controls on hydromorphology, ecology and their interrelationships should be also a key component in the preparation of restoration plans.

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Table of Contents

Contents: Deliverable 2.2 Part 1

4. Responses of macroinvertebrates to Hydromorphology at Multiple Scales

4.1 Macroinvertebrates

4.1.1 Introduction

Understanding and interpreting the patterns and processes of river ecosystems at different hierarchical levels of organization constitutes a basic challenge for managing and restoring their good ecological status. The theory of the hierarchy (O´Neill et al 1986), and the associated concept of scale (Weins, 1989; Levin, 1992; Frissel et al., 1986; Hildrew & Giller, 1994), provides a strong interdisciplinary framework for achieving this understanding, as it incorporates relational links between the different nested spatio – temporal scales.

The Hierarchy of spatial scales for the European Framework for Hydromorphology, presented in a previous Reform delivery (D2.1), includes indicative spatial dimensions and timescales over which these hierarchical HYMO units are likely to persist. Biological communities are linked to this Framework though their composition structure and functioning at different spatio-temporal levels. Therefore, the biotic response to HYMO pressures and processes should be analysed at all scales, because when the assessment of ecological status is done limited at a certain scale, it neglects the fact that both physical habitat and the biological functioning depend on the process scale of boundary conditions.

Macroinvertebrates are often most diverse, abundant and functionally important animal communities in many fluvial ecosystems. The integrity of the freshwater systems depends on how various benthic species make their living and contribute to complex food webs (Covich et al. 1999). Benthic invertebrates respond to habitat alterations and environmental changes, generally due to alterations in the complex connections among sediment-dwelling species and associated food webs or to disturbances, such as floods or droughts.

Due to their relatively small size, macroinvertebrates located in microhabitats and are often patchily distributed and relatively difficult to sample. Data collection and sampling typically used in benthic invertebrate's distribution studies are often done at scales which not adequately tie in the hierarchical context (Parsons et al. 2004).

The objectives of this section are to consider:

- The distribution of relevant fluvial properties, forms and processes within this Hierarchy of Spatial Scales Framework in order to understand and assess HYMO responses to human impacts and restoration
- The incorporation of the macroinvertebrate response into this hierarchical framework

The boundary conditions for a certain landscape or river pattern are given by the large scale, regional–continental or even global acting processes (Habersack, 2000). The patterns derived from catchment scale processes contribute to the boundary condition for processes at the regional and landscape scale (Figure 1).

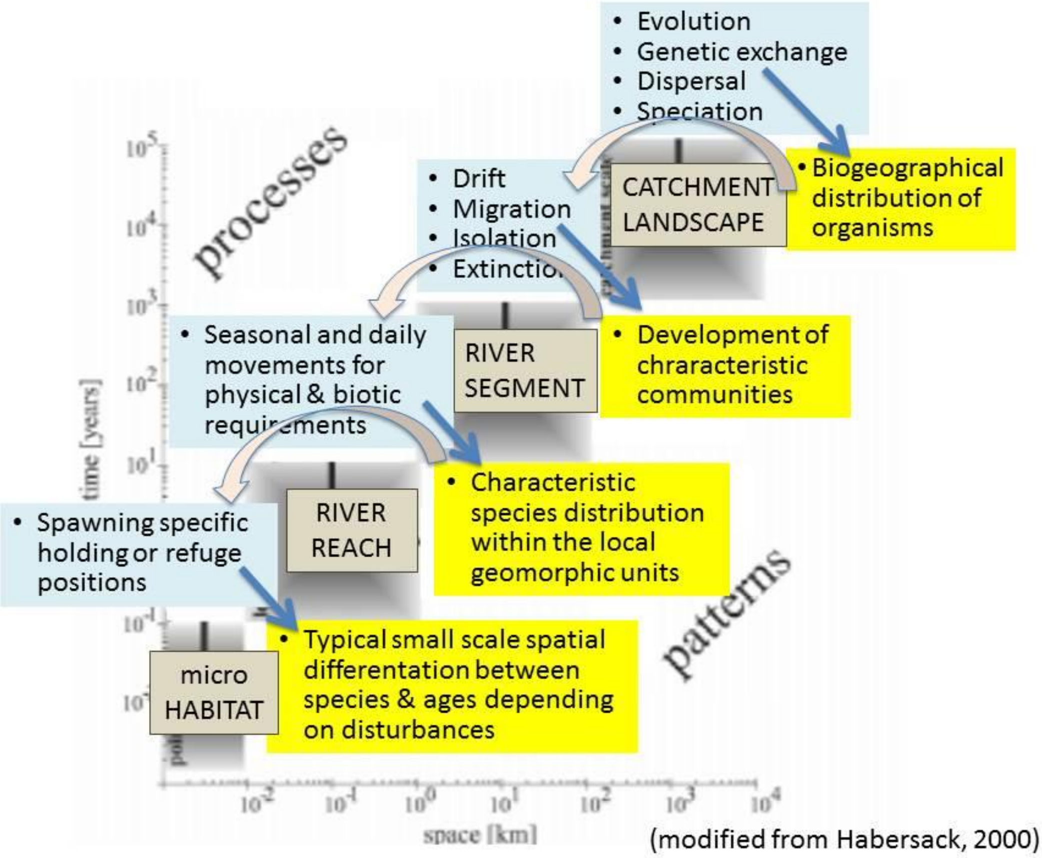


Figure 1.- Biotic processes and patterns at various scales: the boundary conditions for units at a certain scale are given by processes acting at larger scale.

4.1.2 Biological levels of response

Poff (1997) established that the local community structure can be seen as the result of a continuous sorting process through environmental filters ranging from regional or catchment-wide processes, involving speciation, geological history and climate, through intermediate scales where biotic interactions and dispersal-related effects determinate meta-community structure, to the small-scale characteristics of individual patches, such as local predation risk, substratum porosity and current velocity. Malmqvist (2002) reviewed the invertebrate literature with respect to patterns and processes in fluvial ecosystems and showed that the distribution of invertebrates in fluvial habitats is governed by different factors that typically act at different scales.

At a small scale the basic physical conditions at a particular habitat (substrate calibre and structure in a small patch) depends on processes at larger scales in the river network (Frissell et al., 1986; Minshall, 1988). Other physical habitat conditions vary spatio-temporally, and the biological response is adapted to them. However, by contrast small reaches with peculiar conditions may also affect larger-scale habitats. For instance, a local reach with nutrient enrichment, or with different geological traits may release enhance grazer or calcophilous species that will drift and colonize a larger stream reach with different characteristics. This means that although, the type of ecosystem or community control depends on the scale referred to, the biological response offers a buffer system to the physical scale hierarchy Malmqvist (2002).

It is worth stressing that, according to many authors (e.g. Wyżga et al. 2012) biological diversity (or taxonomic composition) of the invertebrate communities in river ecosystems may be unrelated or weakly related strictly to physico-chemical parameters (although they are important for peculiar taxa and community as the whole), which consistently pointed to the high water quality. Instead, the diversity is positively correlated with the degree of variation in physical habitat parameters and is best predicted by the spatial heterogeneity of the cross-section, especially the number of low-flow channels in the case of mountain and sub-mountain rivers. The diversity is generally positively correlated with the degree of spatial heterogeneity - for sure not always and it is not the only factor determining the taxonomic differentiation. But we can find many works supporting that idea and not so much denying, or even questioning it (Feld et al. 2014, Louhi et al. 2011, Palmer et al. 2010).

These issues of different scale respond raise the question about the validity of data from communities and populations studied until now. Among fluvial biologists (Hildrew & Giller, 1994) there is a concern about the sampling scale at which macroinvertebrates are usually collected. It is not only a question of taking into account occupied habitat size, but also the scale that is required for an adequate understanding of both the organisms and the processes in which they are involved.

Therefore, we must consider not only at what scale certain populations or different communities are distributed, but also how their controlling processes might change across several spatial and temporal scales. Observations at a range of scales are helpful in indicating the ways in which patterns, and hence processes, vary with a change of scale, and, therefore, at what particular scale the process of interest could best be studied (Malmqvist, 2002). We may consider different spatial nested scales and link them to significant HYMO processes and associated biological traits. To achieve this, we propose the following scheme (see D2.1):

1. **Region:** The Macro-climate (Biogeographical Region) in which a macroinvertebrate fauna that is adapted to its regional climate and geographic traits is found and shares a common evolutionary history. Illies (1978) in the *Limnofauna Europaea* defined the main aquatic biogeographical regions across Europe. Climate and geological traits are not the only factors that determine the present distribution of fluvial organisms. The evolutionary history of the different macroinvertebrate taxa is also a key factor. Historical events explain the presence or absence of certain taxa within different regions. Also, the terrestrial or marine origins of taxa explains their dominance or rarity in headwater streams or lowland rivers. Crustaceans, prosobranch gastropods and bivalves have a marine origin and their freshwater species tend to be more abundant in lowland rivers. In contrast, Plecoptera, Trichoptera and some families of Ephemeroptera evolved in high mountain streams (Hynes, 1970; Lancester & Downes, 2013).
2. **Catchment** This is a hydrologic spatial unit that is drained by a river network and it is characterized by a Macro-climate (Biogeographical Sub-Region), and average conditions of topography, geology and land cover. Physical processes in catchments

determine the river network characteristics that directly affect macroinvertebrates. The river network presents an asymmetrical system with a multi-factor longitudinal continuous gradient, where upstream conditions and processes affect more intensively downstream ones (Vannote et al 1980). However, from macroinvertebrate point of view the river continue is unique, patchy, and hierarchically discontinuous from headwaters to river mouth, but with a clear general trend. Biological response to this trend or gradient determines different macrobenthic communities from rhithron (cold headwater stream species) to potamon (warm water lowland species) types, representing an ecological gradient or 'zonation' that was defined for its faunistic composition by Illies & Botosaneanu (1963).

3. **Landscape** Within the catchment we focus on the river and its valley. These riverine landscapes result from the dynamic interactions of spatially-nested river corridor sections that are also influenced by hill slopes close to river. Meso-climate, elevation, topography, geology, land uses and soil conditions of each landscape determine the type of fluvial corridor. The presence of riparian corridors is responsible for the type of benthic communities living within each landscape unit. In particular, riparian corridors control the input of organic matter (CPOM; DOM) and wood (Cummins, 1973; Hawkins et al., 1982). This organic matter is the main food source for most benthic invertebrates (shredders, gatherers and filter feeders), and so the macrobenthic trophic structure is controlled by riparian corridors (Dudgeon, 1988 and Basaguren et al. 1996).

Absence of riparian vegetation on the contrary will promote primary producers and benthic invertebrates will have different structure, often dominated by grazers. However, at this scale meta-community structure is determined not only by local abiotic environmental conditions but mainly by biotic interactions and dispersal-related effects (Heino, 2013).

4. **Segment** Each fluvial landscape consists of a series of alternating segments with different geomorphological traits. Each tributary junction of the river network causes a discontinuity in the river's physical characteristics and interrupts the expected pattern of downstream transitions. Segments may also be differentiated by shifts in geology, topography, groundwater springs, or in the valley type / form. Fluvial segments are subject to internally uniform flow regimes and a consistent set of river channel types. As a result, they show similar functional relationships between forms and processes. Populations and communities of macroinvertebrates within each segment correspond to those adapted to the prevalent HYMO processes (erosion, deposition and transport).

5. **Reach** Along each river segment the thalweg rises and falls, corresponding, for example, to reaches dominated by rapids alternating with those dominated by pools. These are often called meso-habitats. Cross sectional form, sedimentary structure, channel gradient and hydraulic conditions are the main features that characterize a reach and thus, their benthic communities, for example lentic and lotic macroinvertebrate species. In floodplain rivers, secondary channels, oxbows and abandoned meanders may be present. These wetland and palustrine areas host particular macroinvertebrate communities that are different from those inhabiting in the main channel. One of the most important factors connected with the reach-level of river organization is the number of channel threads (low-flow channels

in the case of mountain and sub-mountain streams). Reaches that contain multiple low flow threads are usually associated with larger aggregated channel width and with finer material on the bed surface. The difference in bed-material grain size between a narrow, single-channel section and a wide, multi-thread section can be primarily attributed to differences in unit stream power, especially during flood flows, when the gravelly substrate material can be mobilised, transported and hydraulically sorted. Spatial variability in grain size of the surface layer bed material increases during low and medium flows due to the deposition of fine sediments on the bed of less active channels in a multi-thread system. Single-channel sections most often exhibit relatively small differences in hydromorphological conditions among cross-sections, with similar averages of the physical parameters, and small coefficients of variation. In the multi-thread cross-sections of mountain and sub-mountain streams (and lowland rivers with high flow velocity), low-flow channels with fast-flowing water and a gravel bed are usually accompanied by others with a relatively slower current and a bed covered with sand or silt, increasing the chances of colonization by various macroinvertebrates. Many studies have shown that the diversity of benthic invertebrate communities is determined by low-flow channel width and the variation in flow depth, velocity and bed material size. The increased number of flow-threads in a cross-section is associated with a larger aggregated width of low-flow channels and a greater complexity of physical habitat conditions. For example, research by Wyżga at al. (2011) in the Czarny Dunajec (Polish Carpathians),has shown that single-thread cross-sections host four to seven invertebrate taxa, mostly eurythopic, which represented two or three functional feeding groups. In multithread cross-sections, seven to nineteen taxa were recorded, with the assemblages representing all five functional groups (scrapers/grazers, shredders, collectors-gatherers, collectors-filterers and predators), and with taxa typical of both lentic and lotic habitats. Widely tolerant perlodid stoneflies (*Perlodes* sp.) and stoneflies (*Perla* sp.) were most commonly found in single-channel sections, the former being recorded in five and the latter in four investigated cross sections. In turn, limnophilic taxa, such as *Nematoda* pl.sp., Lumbricidae, *Chironomus* sp. and *Tabanus* sp.,were completely absent in these sections. Surprisingly rare were rheophilic taxa, such as *Crenobia alpina*, *Heptagenia* sp., *Goera* sp. and river limpet *Ancylus fluviatilis*, with the first taxon recorded in two single-thread cross sections, and the remaining ones in a single cross section. Finally, of the five functional groups of benthic inverterbartes, only predators and shredders were found in the surveyed single-thread cross sections, and one additional group (filter feeders or gatherers) was also represented in five of these cross sections. In single-thread cross sections, the grain size of the cobble bed proved to be unrelated to base flow velocities, as the bed is formed at substantially higher velocities during high flows, especially flash floods. At the same time, the shallow-water, low-velocity areas within the cross sections lacked fine bed sediments. This indicates that shallow-depth and slow-flow conditions are transient in these cross sections and fine sediments, even if deposited on the bed at low to moderate flows, are readily and regularly flushed out from such sites. On the other hand, in multithread cross sections two populations of bed material were identified: (1) pebble to cobble sediments, which predominated in the main braids conveying most of the discharge and (2) muddy-sandy sediments, which usually occurred in the lateral braids that exhibited slower flow velocities, but also in the low-velocity areas within the main braids. Grain size generally reflects depositional conditions or lag deposits retained during flood flows, but the latter are adjusted to hydraulic conditions at low and moderate flows. When there is a relatively long-lasting disconnection of the upstream end of lateral braids and anabranches from the main water current, fine sediments overlying gravelly material can persist and accumulate, at times attaining quite a considerable thickness. The high heterogeneity of habitat conditions in multithread channel sections is linked to specific combinations of hydraulic and bed substrate conditions, suitable for different macroinvertebrate taxa (Wyżga at al., 2011).

6. **Geomorphic Unit** At the micro-scale reaches contain microhabitats. Each Geomorphic Unit presents a different combination of different types of substrate (boulder, gravel , sand, silt, woody debris, macrophytes), hydraulic conditions, food resources, and interstitial environments. Habitat requirements of macroinvertebrates may be very specific, and within the same species may vary with their stage of development. Many geomorphic units may be found in a reach, but with only a few species in each one. From a different perspective, Geomorphic units are the potential niches that can be occupied. Thus, a more heterogeneous reach may accommodate a greater number of different Geomorphic Units and so may sustain a higher biodiversity. The types of microhabitats are generally repeatable, although their classification may be difficult as a result of highly subjective assessments by different observers. Moreover, macroinvertebrates in different type of reaches have unequal chances of avoiding flushing downstream by flood flows, and this may result in dissimilar decreases in the taxonomic richness of invertebrate communities during floods (Brookes et al 2005). We may expect that higher microhabitat differentiation is an important factor for increasing the biological diversity and species richness.

At reach scale, it is generally well established that water depth, velocity and substrate grain size are the primary components of physical habitat in running waters, which appear to be the best predictors of benthic invertebrate distribution (e.g. Beisel at al. 1998). While at microhabitat level, other hydraulic parameters, more complex, together with sedimentary variables, describe conditions in the water column immediately above and on the river bed (e.g. Froude number, shear stress, Shields entrainment function) and are related to benthic invertebrate populations (Rempel et al. 2000).

This theoretical framework that links the distribution of macroinvertebrate communities and environmental influences across a hierarchy of spatial scales of river system organization has been rarely evaluated in a holistic study, although several studies have used a more limited range of spatial scales. One exception is the research by Parsson et al. (2003) within the Murrumbidgee River catchment (Australia). They examined the associations between macroinvertebrate assemblage distribution and environmental influences across the whole hierarchy of river system organization. They sampled macroinvertebrates according to a nested hierarchical design incorporating 4 geomorphologically derived scales: catchment, zone (similar to segment), reach, and riffle. Macroinvertebrate assemblages were similar among riffles within a reach, but were dissimilar at the zone and catchment scales.

Similarity among assemblages in riffles within reaches is an obvious consequence of the relative homogeneity of riffle morphology, and such results have been also reported by Rabeni et al. (1999). However, other studies have reported differences in macroinvertebrate assemblages among adjacent riffles (Barmuta 1989, Downes et al. 1995, Mermillod-Blondin et al. 2000) or among patches within a riffle (Downes et al.

1993). However, because Parsson et al. (2003) considered the similarity among riffle communities across a continuum of multiple scales, their variability had less significance in relative terms.

Macroinvertebrate assemblages were generally dissimilar among 'zones' (defined by authors by channel confinement caused by valley shape) suggesting that mesohabitat assemblages were not influenced by the effects of valley morphology on channel geomorphology (sediment transport, or hydrologic regime traits). Maridet et al. (1998) also found that valley shape explained only minor differences in macrobenthic assemblages distribution.

Also for larger scale units, Parsson et al. (2003) found low between- and within-catchment assemblage similarity. This lack of congruence between catchments and faunal distributions suggests that macroinvertebrates do not respond to the homogeneity of physical conditions provided within catchments.

The distribution of macroinvertebrate communities may present a regional-scale pattern larger than the average catchment size or scale. Ecoregions represent broad-scale areas with similarities in climate, geology, vegetation, soils, physiography and biogeography to which biota may respond. Also, different Ecoregions may overlap different river basins and large catchments may intersect more than one ecoregion and include several catchments. A frequent example is a mountain range that is an ecoregion but its different slopes belong to different catchments. These circumstances provoke a controversy among different studies: Feminella (2000), Oswood et al. (2000), and Van Sickle, Hughes (2000) and Mykrä et al. (2004) found that faunal congruence among ecoregions was greater than that obtained for catchments, as was the case for Murrumbidgee catchment, whereas Hawkins and Vinson (2000), McCormick et al. (2000), Marchant et al. (2000), and Waite et al. (2000) encountered the opposite.

Parsson et al. (2003) found three different regions within the Murrumbidgee catchment. They divided the macroinvertebrate data by region and then the analysis revealed a relationship between macroinvertebrate distribution and the catchment and zone scales of river system organization.

In a later study also on the Murrumbidgee, Parsson & Thoms (2006) related different scaled environmental factors (measured across a hierarchy of scales) to different cluster levels of macroinvertebrate distribution. They found that an hierarchical pattern of region-level and reach-level macroinvertebrate distribution was matched by a catchment-scale and reach-scale distribution of environmental influences. However the Intermediate zone-scale environmental factors and smaller riffle-scale factors were not important influences on macroinvertebrate distributions. It is difficult to transfer the results of this study to the hierarchical framework devised within REFORM because of differences in the way reaches are defined (Parsson et al.(2003) define 'reaches' by tributary junctions) and because 'reaches are not necessarily nested within 'zones' (Valley confinement criteria) as they are in the REFORM framework (see Deliverable 2.1).

Richards et al. (1997) identified relationships (quantified predictive models) between macroinvertebrate community's traits and reach/landscape-scale attributes in Midwestern USA catchments. These relationships proved how landscapes influenced species assemblages at multiple scales. They found that reach scale properties were highly predictive of species traits. Cross-section area, % shallow, slow-water habitats and % of fine sediments were the most important variables, but also life history and behavioral attributes exhibit strong relationships at local conditions. On the contrary, catchment-scale variables had few significant models with species traits (only surficial geology and associated land uses).

Hering et al. (2006) in a comparative analysis of biological elements assessing stream ecological status across Europe found that all organism groups responded to land use changes to varying degrees and t hydromorphological degradation at the microhabitat scale, while the response to hydromorphological gradients at the reach scale was mainly limited to benthic macroinvertebrates. Thus, macroinvertebrate response was effective along the whole fluvial longitudinal gradient at reach and microhabitat scales. Nevertheless, Herings study incorporated a strong anthropogenic disturbance gradient (especially due to land use), which may have overruled hymo effects).

River zonation: At catchment level we may consider only the river basin network and differentiate between headwater streams, piedmont and lowland rivers. HYMO variables (slope, width, flow, substrate calibre) are not the only factors controlling the macrobenthic distribution across river zones, but also thermal conditions (see Figure 2).

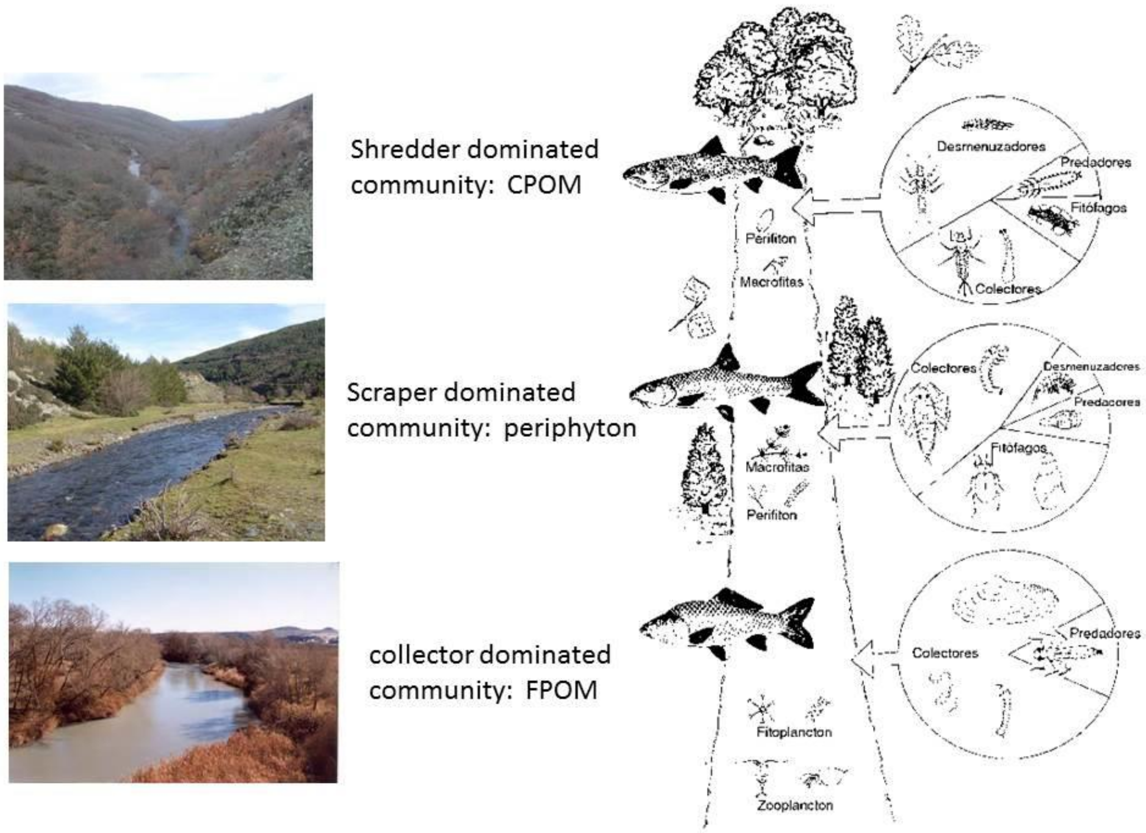


Figure 2.- River continuum and different macroinvertebrate communities along the altitudinal gradient: TROPHIC STRUCTURE at different Landscape units.

The following text describes several studies that have attempted to identify differences in macroinvertebrates along rivers and within different spatial units.

Heino et al. (2004) studied patchiness in benthic macroinvertebrate abundance and functional feeding group (FFG) composition in a boreal river system at three spatially nested scales in three tributaries, with two stream sections (orders) within each tributary, three riffles within each section, and ten benthic samples in each riffle. They found that most of the variation in total macroinvertebrate abundance, abundances of FFGs, and number of taxa was accounted for by the among-riffle and among-sample scales. Such small-scale variability reflected similar patterns of variation in in-stream variables (moss cover, particle size, current velocity and depth). FFG composition of the macroinvertebrate assemblages differed significantly among tributaries and stream sections being more variable than those in higher stream order.

Mykrä et al (2004) examined the variation in several macroinvertebrate ecological attributes and environmental variables at three hierarchical scales (ecoregions, drainage systems, streams) in Finland. They found significant spatial variability in most of the macroinvertebrate metrics and environmental variables. Nevertheless, for most metrics, ecoregions explained more variation than drainage systems. Li et al., 2001 studied the variability in macroinvertebrate assemblages (richness, density, composition in Ephemeroptera, Plecoptera and Trichoptera, dominance and diversity) at seven spatial scales in 16 streams in Oregon, USA. Landscape level, ecoregion and among-streams components accounted for most of the variance.

Boyero & Bailey (2001) studied the variability of benthic macroinvertebrate communities at three spatial nested scales within streams in Panama. They found that density and richness showed greater variation among stream orders and within riffles, while individual taxa varied mostly among and within riffles, and community evenness varied within riffles. Water velocity was strongly related to the variability of macroinvertebrate metrics. Riffles were more heterogeneous in composition within first order than within second or third orders streams.

Kubosova et al. (2010) evaluated the preference of macroinvertebrate taxa for channel units of the Becva River. The studied river stretch was renaturalized by a flood event which increased habitat diversity in the marginal zone of a widened channel in comparison with a regulated part. Channel habitats were classified in two steps into the central part of the channel (subsequently further divided by hydraulic thresholds described by Jowet (1993)) and marginal habitats (further distinguished as main channel margins and side arms). Channel margin habitats were mainly defined by ‘‘negative’’ indicator taxa (classification of samples was caused by non-occurrence and low abundances of certain taxa in this habitat). In general, there was only a small group of taxa that preferred these habitats. Taxa were not fully habitat specific because they mostly occurred in two or three habitat types. This could be the result of autecological plasticity of individual taxa and connectivity among habitats.

Brabec et al. (2004) described differences in macroinvertebrate characteristics (metrics) between riffle and pool habitats of streams covering a gradient of organic pollution. A significantly higher proportion of taxa were found to prefer a stony substrate, high current velocity, with a proportion of filter feeders and grazers, a number of Coleoptera taxa and a relatively greater abundance of EPT taxa in riffles. In contrast the Saprobic Index, the proportion of active filter feeders, those with a POM habitat preference, and a relatively higher abundance of Diptera were found in pool habitats.

4.1.3 Contribution of macroinvertebrates to sediment dynamics

HYMO conditions are not the only controls on macroinvertebrate communities (Covich et al. 1999). Macroinvertebrates may also act as bio-engineers changing the HYMO traits of their habitats. Indeed, macrobenthic animals actively contribute to gravel and sand erosion and transport in streams favoring habitats formed by dynamic patches. Their activity mainly affects:

- transport of gravel at baseflows
- sediment surface characteristics
- the critical shear stress necessary to induce gravel motion during floods

Statzner & Peltret (2005) and Statzner (2012) have typified the way in which macroinvertebrates function as bioturbators (crayfish) or bioconsolidators (cadis-netspinnig). Bioconsolidators are rarer (in the terms of taxonomic richness and their biomass) than bioturbators, since the influence on riverbed properties is more strongly linked to the latter functional group. In strictly ecological terms it is very similar to the action of "shredders".They feed on large fragments of detritus - CPOM (more than 1 millimeter) – crayfish is the typical example of such shedder– or water plants The result of their activity is the disintegration of organic matter and an increase in FPOM. Examples of bioconsolidating macroinvertebrates are: caddis-flies (*Limnephilus*, *Halesus*, *Anabolia* pl.sp.); stoneflies (*Plecoptera*); small crustaceans (amphipods, copepods); true flies; and snails.

The role of macroinvertebrates in the shaping riverbed sediment structure may be irrespective of their feeding behavior. For example, during dry periods and low water levels, the useable area covered by microhabitats suitable for particular taxa may decrease and, as a result, the same number of individuals begin to disturb one another, leading to the release of particles. Such situation is especially important in the case of large invertebrates, for example *Perla* sp. stoneflies, which quite often live side by side.

The contribution of macroinvertebrates to sediment dynamics may also be linked to the changes in the ecosystems' trophic structure, resulting from flow changes (flow reduction or flood flows). For example, a lack of net-building caddis-flies due to their flushing downstream may result in increased bioturbation. Such relations are highly unpredictable, because of particular phenomena that depend on the species structure and the various types of defensive mechanisms that are adopted as anti-flush "security" mechanisms. Attrill et al. (1996) give the example of Andodonta complanata, which disappeared from a community within a month of an the initial reduction in flows, but returned when full flow conditions were restored. Asellidae, on the other hand, disappeared for a longer time. Chironomidae and Tubificidae, which may induce the sediment movements when in high abundance and concentration in mud deposits, experience high differences in their presence / abundance between drought and post-drought periods (Boix et al., 2010). Another example of a similar relation is represented by the rapid increase in the number of filter feeders during long-duration low flows. This results in a change in near-bed sediments, particularly suspensions (Extence 1981).

4.1.4 Habitat requirements

Local species pool

The response of macroinvertebrates to HYMO conditions has been well studied at the local scale. Concerning stream macroinvertebrates, physical constraints (hydraulics, particle size and many other environmental drivers) typically play a predominant role in comparison to other niche dimensions (Statzner, 2008). However, macrobenthic communities at microhabitat scale potentially depend also on biological factors such as social behaviour, gregarism, predation, competition, recent history of the microhabitat (Lancaster & Downes, 2010).

The studies of Dolédec et al. (2007) and Mérigoux et al. (2009) provide a general picture of the degree of variation in abundance-environment relationships (AERs) among sites and sampling occasions. Many taxa, defined at different biological levels, have repeatable AERs at sites on rivers with different size, geology, water quality, community composition and other ecological characteristics. However, other taxa (examples in Mérigoux et al., 2009) have highly variable AERs. For example, of 151 taxa studied by Dolédec et al. (2007), 14 taxa have a generalized (site-averaged) AER that explains >50% of their log-density variations among microhabitats (within sites), and 40 taxa have AERs that explain > 30% of their density variations. Two-thirds of the variability in density explained by site-specific AERs are accounted for by a site-averaged, generalized AER in small German streams (Dolédec et al., 2007), as well as in large French streams (Mérigoux et al., 2009). Jowett and Davey (2007) also showed that generalized additive models explained about 50% of the abundance variation of benthic invertebrates taxa in 6 New Zealand rivers. Therefore, the fact that hydraulics may explain >50% of density variations among microhabitats within multiple sites with contrasting characteristics is remarkable, and suggests the existence of strong causal mechanisms even if the details of these mechanisms are not fully known and require further study (Lamoroux et al., 2010).
Different macroinvertebrate taxa and delopement stages has different HYMO requirements (see D 1.3). Every microhabitat type, characterized mainly by hydraulic conditions and substrate type, may be linked to one or several macroinvertebrate taxa that often occur together. This is consequence of the fact that the microhabitat's features fulfil the species or species assemblage physical requirements for living. Main macrobenthic requirements deal with water velocity, substrate, suspended solids, and interstitial environment:

a. <u>Water velocity</u>: Benthic invertebrates do not respond directly to flow conditions, they rather respond to water velocity and drag forces (Statzner et al. 1988). The adaptation of species to these hydraulic variables allow them to be classified into lentic and lotic species.

This classification, although in common use, is not adaptable to some peculiar conditions. According to the basic definition, lotic habitats are flowing-water habitats, such as those of rivers and streams. The turbulence of flowing waters provides a natural means of aerating, thus making oxygen readily available to animal life. Other terms of peculiar importance, connected with the lotic habitats, are erosional zone and depositional zone. An erosional zone is an area in which the water velocity is fast enough to carry small particles in suspension. This zone is often typified by riffles and the river bed is devoid of silt The bed generally consists of stones, gravel and sand, depending on the typical flow velocity (gravel and stones may be transported by high flow velocities). A depositional zone is an area in which the current is relatively slow and small particles fall out of suspension and become deposited as silt on the bed. Such areas often predominate in wider streams. Stream pools, slow reaches, backwaters and slow edgewaters are typically depositional in nature. These slower flowing areas may be expected to host fewer bottom-dwelling invertebrate species than riffle areas, but sometimes they have large numbers of a few dominant taxa.

Lentic habitats are according to standard definitions, standing waters (lakes, ponds, swamps). But sometimes this term is being used for stagnant reaches of the streams or rivers, particularly side branches. Such habitats may be inhabited by the specific invertebrate taxa (basically Chronomidae and Tabanidae), but during the high flows they are supplied with other invertebrates, such as larvae of mayflies, dragonflies, stoneflies or caddis-flies, which may be able to persist in that habitat (Cummings et.al.1966).

Jowet (1993) classified stream habitats using Froude number thresholds into riffles, runs and pools. Macroinvertebrate preferences associated with these habitats are described by Syrovatka et al. (2009), Kubosova et al. (2010).

Syrovatka et al. (2009) compared chironomids and oligochaets in terms of their distribution among river habitats. The main gradient reflecting the taxonomic composition of both groups could be explained by hydraulic conditions and, inversely, by the amount of deposited particulate organic matter (POM). Although the total abundance of both oligochaetes and chironomids was independent of hydraulic conditions, only a few oligochaete taxa were able to succeed in hydraulically rough conditions and most oligochaete taxa were found only in pools. Chironomids showed high taxa richness, which seemed to be limited by the quantity of the available food and space resources rather than hydraulic stress.

Based on observations from the Becva river, Syrovatka & Brabec (2010) reported that 47 % of the variability in the chironomid taxonomic composition could be explained by hydraulic conditions.

b. Substrate type: habitat requirements of benthic invertebrates are strongly determined by substrate type. As a result, limnologist have traditionally used classifications of substrate types to define micro-habitats (Table 1). The majority of river invertebrates are benthic ones. This term includes the typical bottom dwellers, but is commonly extended to include any taxa that reside on or in any substrate within the aquatic habitat. Substrates with which benthic invertebrates may be associated include not only bottom surfaces but also any fixed or floating inorganic or organic object – e.g. stems of aquatic plants, driftwood, rock outcroppings.

Benthic organisms that cling steadfastly to substrates in fast flowing waters are termed clingers. Many of them are equipped with grasping tarsal claws (e.g. riffle beetles or some larval minnowlike mayflies) or with anal claws or hooks at the end of the abdomen (larvae of some net-spinning caddis-flies, midges). Many rheophilic taxa, living in fast flowing rivers, have a low profile or highly streamlined body that minimizes the frictional force of water. The other way to reduce that force is to orient the body in relation to the current.

Benthic invertebrates that crawl about on various sufaces of rocks, fine sediments, woody debris or leaf packs are termed sprawlers. Many of them commonly reside on the undersides of rocks (e.g. larvae of flatheaded mayflies or stoneflies) or in porous areas of rocks or debris (e.g. larvae of some midges or spiny crawling mayflies). Some (mainly sand-dwelling) sprawlers often become partially covered with sediment.

The invertebrate taxa that commonly reside on aquatic plant stems, root systems alongside the bank, filamentous algae or mosses are termed climbers. They usually inhabit the slower reaches or marginal waters of the rivers – very often among the vegetation. Most are adapted for climbing, but some occasionally swim from one substrate to another. Others are relatively stationary. Examples of this category are the larvae of many dragonflies, damselflies and some aquatic caterpillars (McCafferty 1998).

Table 1 - Natural choriotop types describing river bottom substrate and micro-habitats

Table IV. Natural choriotop types describing river bottom (modified from Austrian Standard ÖNORM 6232)

Nomenclature	Grain size range	Choriotop description
Megalithal	>40 cm	Upper sides of large cobbles and blocks, bedrock
Macrolithal	>20–40 cm	Coarse blocks, head-sized cobbles, variable percentages of cobbles, gravel and sand
Mesolithal	>6.3–20 cm	Fist to hand-sized cobbles with a variable percentage of gravel and sand
Microlithal	>2–6.3 cm	Coarse gravel, (size of a pigeon egg to child's fist) with percentages of medium to fine gravel
Akal	>2 mm–2 cm	Fine to medium-sized gravel
Psammal	0.063–2 mm	Sand
Pelal	<0.063 mm	Silt, loam, clay and sludge
Biotic choriotop		
Detritus		Deposits of particulate organic matter; distinguished are: CPOM (coarse particulate organic matter), as for example, fallen leaves and FPOM (fine particulate organic matter)
Xylal		Tree trunks (dead wood), branches, roots, etc.
Sapropel		Sludge
Phytal		Submerged plants, floating stands or mats, lawns of bacteria or fungi, tufts, often with aggregations of detritus, moss or algal mats (interphytal: habitat within a vegetation stand, plant mats or clumps)
Debris		Organic and inorganic matter deposited within the splash zone area by wave motion and changing water levels, for example, mussel shells, snail shells

c. <u>Interstitial environment:</u> Benthic invertebrates that burrow into soft bottom substrates and live in this interstitial habitat are termed burrowers. The substrate is usually silt, clay or silt-sand. The burrowers are linked to slower flowing reaches and bank zones of rivers. Examples of this category include the larvae of burrowing mayflies, caddis-flies and midges (McCafferty 1998).

d. <u>Suspended solids:</u> Benthic macroinvertebrates are able to withstand short-term increases in suspended and benthic sediments, as these are natural conditions were species have evolved. Even, there are species adapted to live under high fine sediment loads or over silty bottoms, as some species of Chironomidae, Oligochaeta or Sphaeriidae . However, continuous high levels of sediment input, often associated with farming and mining activity, may completely change the natural faunal assemblage. Wood & Armitage (1987) have reviewed the effects of fine sediments on lotic systems and have conclude a reduction on abundance, diversity and biomass of affected macroinvertebrate assemblages, being the guilds of filter feeders the one most impacted.

Fine sediment suspension and deposition affects benthic invertebrates in four ways (Wood & Armitage (1987):

- altering substrate composition and changing the suitability of the substrate for some taxa.
- increasing drift due to sediment deposition or substrate instability

- affecting respiration due to the deposition of silt on respiration structures or low oxygen concentrations associated with silt deposits.
- affecting feeding activities by impeding filter feeding due to an increase in suspended sediment concentrations, reducing the food value of periphyton and reducing the density of prey items.

Regional species pool

The bio-geographical concept of hierarchical faunal filters (Poff 1997) establishes a filtering process from the regional pool of species to the species living in a local habitat or in a microhabitat. However, as we upscale to segment or landscape levels the species filtering process is difficult to understand from HYMO factors alone. In Table 2 these possible filtering processes are shown at different scales

Other factors apart from HYMO factors may be more influential:

- Trophic structure within different Landscape units may result in grazing dominated communities in rivers crossing open valleys with riverbanks formed by grasslands or shrublands, and shredder dominated ones in forested river corridors and in rivers within narrow valleys.
- Temperature, particularly differences in air and water temperatures have enormous effects on aquatic insect life cycles.

Table 2 - Scale-dependent influences of water-related physical processes that determine the macroinvertebrate community according to their hydromorphological requirements

	Biogeographical context	HYMO Requirements				Trophic resources	Fluvial Disturbance
		Velocity	Substrate	Interstitial	Suspended solids		
Region	**Pool of potential native species**						
Catchment	Pool of potential native species				Hillslope erosion	Woody debris	Temperature L. gradients
Landscape Unit	Pool of potential native species				Vegetation cover	Riparian corridor	
Segment	Enviromental filters	Mean channel slope		Gravels	Channel Dynamism	Guild structure	Pioneer vs. mature communities
Reach	Enviromental filters	Lentic & lotic species	Lithal & Psammal & Pelal	Akal	Siltation tolerant species	Schredders, collectors and scrapers	Pioneer or Mature community
Geomorphic Unit	Local species Pool	Shear stress Boundary layer	Lithal or Psammal or Pelal	Akal	Siltation tolerant species	Schredders, collectors and scrapers	Pioneer or Mature community

4.1.5 Hymo processes associated with macroinvertebrates

Geomorphic Adjustments and changes

1. Single channel vs. braided

Multi-braided channels may have greater heterogeneity of over the single ones, and this may be linked to the abundance of microhabitats and substrate diversity. It also increase length of aquatic-terrestrial transition zone (ecotone) associated with high intensity of biogeochemical processes (mineralization) and high spatial heterogeneity of environmental conditions (water temperature, conductivity, dissolved oxygen). Nevertheless, multi-braided channels are often unstable habitats, due to the fact that are associated to intense sedimentation processes. Under this substrate instability, benthic abundances and diversity are significant lower.

2. Spatial heterogeneity – Restoration and renaturalization of streams can be associated with recovery of channel forming processes. It accelerates dynamics of lateral and vertical erosion/sedimentation and substrate redistribution driven by discharge pattern. Changes of spatial heterogeneity are usually the most distinct in bank zone where patches of vegetation, gravel bar, fine sediments and course particulate organic matter represent more diverse conditions than regulated shoreline usually formed by uniform riprap banks.

3. Fluvial disturbances - These include inundation (depth-duration), sediment deposition (burial), shear stresses / drag imposed on benthic animals (flow velocity gradients), and sediment erosion. These reflect the flow and sediment supply regimes to the river network and are moderated at the segment to reach scale by the valley-channel gradient, the channel style / width (unit stream power) and they also vary across the valley bottom – floodplain.

Processes controlled by macroinvertebrate activity within the Habitat Spatio-Temporal Framework

Biological processes like dispersion drive invertebrate distribution linking different ecological systems across boundaries. The spatial distribution of invertebrates along the fluvial ecosystems is determined not only by habitat conditions, but also to a large extent by active movements of the invertebrates (Figure 3). Spatially separated ecological processes, become linked to each other when macroinvertebrates move in association with needs of feeding, mating and dispersal, when they take place across system boundaries. The importance of such linkages in the riverine landscape, particularly when they take place across system boundaries, are considerable (Nakano & Murakami, 2001).

But also, physical processes are greatly influenced by macroinvertebrate activity:

- cycling of nutrients and carbon
- turnover of organic material
- linkages between the terrestrial and aquatic systems

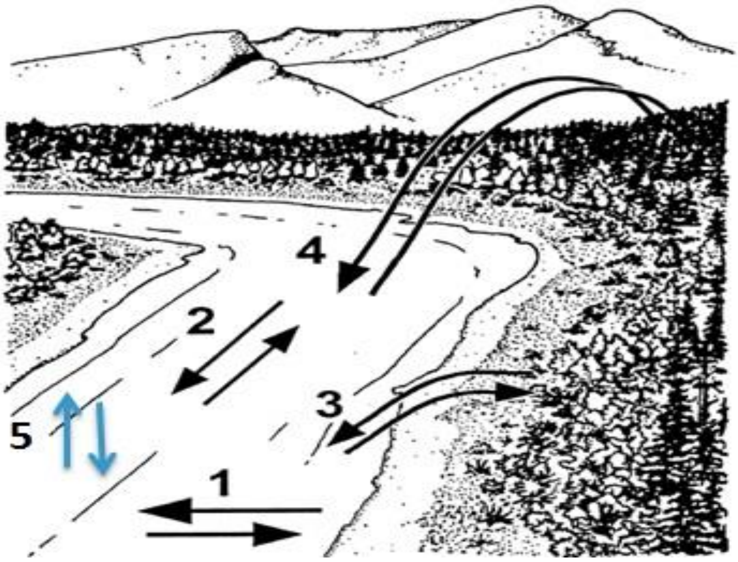


Figure 3 - Pathways of matter flow in fluvial systems (modified from XX): 1) Instream lateral flow. 2) Longitudinal movements. 3) Movements between riparian and aquatic habitats. 4) Long-distance movements between upland and river. 5) Vertical connection of hyporheic with bed surface

4.1.6 Conclusions

We have seen that macroinvertebrates composition, structure and functioning respond to the Hierarchical Framework of spatial scales. However, it is clear that some levels of hierarchical structure are much more important than others for the absence/presence of macroinvertebrates:

- Different Geomorphic units of the same type within the same Reach shows similar macrobenthic composition and structure.
- It is not so clear that each different type of Geomorphic unit type within the same Segment is likely to show similar macrobenthic functioning. Nevertheless, meta-population dispersion along the segment may maintain certain homogeneous composition as results of the same flow regime.
- Each different type of geomorphic unit within the same River Network show a gradient along its continuum: Inefficiencies of upstream processes are the input for the functioning downstream communities.
- Macroinvertebrate faunas show similarities among different watersheds within the same Bioregion, especially along in the mountain ranges that separate basins, but also, the opposite occurs in large river catchments which contain different bioregions.

Therefore, large regions, catchments and local reaches are important levels of organization for fluvial macroinvertebrate-environment associations. We have seen different examples of river basin systems that support the applicability of hierarchy theory to describe the organization of physical– macrobenthic associations in river ecosystems. The multi-scaled approach allows detection of different levels of hierarchical organization, and also shows other asymmetrical traits such as emergent properties through top–down constraints and through bottom–up influences. Finally, the use of the Hierarchical Framework of spatial scales, linking macrobenthic structure with functional hydromorphology, is a basic tool for developing understanding of river ecosystem organization. This understanding will promote a better river conservation and enhance restoration management because it facilitates a holistic, ecosystem perspective rather than a partial, single-scale, single-component or single-discipline perspective.

4.2 Fish

4.2.1 Habitat requirements and life cycle of fish

Fish are rather long-living mobile aquatic organisms which regularly perform various movements up to obligatory migrations and thus use their environment over large spatial and temporal scales (Table 3). Especially the diadromous species, which grow and mature in marine waters and in freshwaters, migrate upstream into the headwaters for spawning or vice versa, use the full freshwater catchment and beyond (McDowall 1997, Lucas & Baras 2001, Alerstam et al. 2003). The entire catchment, which encompasses more than one river region, is also covered by potamodromous species which obligatorily migrate within freshwaters up to headwaters for spawning (Northcote 1997, Lucas & Baras 2001, Fredrich et al. 2003, Jungwirth et al. 2003). The other movements mentioned in Table 3 typically occur within a river section or region except for some compensation or dispersal movements (Detenbeck et al. 1992, Pavlov 1994, Albanese et al. 2009, Radinger & Wolter 2013).

Table 3 - Types of migration with relevant spatial scale a selection of relevant references

Type of migration	Spatial scale	References
obligatory spawning migrations	Region, catchment, landscape unit	McDowall 1997, Northcote 1997, Lucas & Baras 2001, Alerstam et al. 2003, Fredrich et al. 2003, Jungwirth et al. 2003
seasonal and diurnal habitat shifts	Reach, segment	Stott 1961, Molls 1997, Kubecka & Duncan 1998, Koed et al. 2000, 2006, Wolter & Bischoff 2001, Reichard et al. 2003, Fladung 2003, Jungwirth et al. 2003, Hirzinger et al. 2004, Wolter & Freyhof 2004
ontogenetic habitat shifts of juvenile fish	reach	Copp 1992, Freyhof 1998, Garner 1999, Gaudin 2001, Grift 2001, Bischoff 2002, Grift et al. 2003, Schiemer et al. 2003
compensatory movements	Segment, landscape unit, catchment	Detenbeck et al. 1992, Pavlov 1994, Baade & Fredrich 1998, Koed et al. 2000, 2006, Fredrich 2003, Albanese et al. 2009, Hein et al. 2011
dispersal	Landscape unit, catchment	Rodriguez 2002, Winter & Fredrich 2003, Albanese et al. 2009, Hein et al. 2011, Radinger & Wolter 2013

River fishes are especially well adapted to hydromorphological conditions and habitats, for example by evolving gravel spawning in high energy rivers (e.g. Bardonnet 2001, Armstrong & Nislow 2006) and facultative plant spawning on inundated vegetation in low energy floodplain rivers (e.g. Grift 2001, Scharbert 2009). In addition, rough structures, like large stones and wood, depth and width variability, islands, backwaters, and multi-thread channels, and also vegetation in low energy rivers as well as extended floodplains provide natural shelter and refuges from high stream power (Mann 1996, Guégan et al. 1998, Smokorowski & Pratt 2007, Schwartz & Herricks 2008, Snelder & Lamouroux 2010). These habitat structures typically occur in patches within larger functional process zones (Thorp et al. 2006, Lasne et al. 2007). Further, nearly all species have in common the dependency on shallow, slow flowing, and diversely structured littoral areas as nurseries for the emerged offspring (Scheidegger & Bain 1995, Molls 1997, Staas 1997, Freyhof 1998, Garner 1999, Jurajda 1999, Schiemer et al. 2001a, Grift et al. 2003, Hirzinger et al. 2004, Scholten 2013). Therefore, 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, Bardonnet 2001, Schiemer et al. 2003, Armstrong & Nislow 2006). The heterogeneity of the flow structure, particularly the presence of low-transit zones and backwaters, also controls the downstream displacement of fish and determines the availability of shelter and nursing habitats (Wolter & Sukhodolov 2008, Sukhodolov et al. 2009). In contrast, adult life stages typically show higher swimming abilities and environmental tolerance, which enables them to use and switch between various habitats and resources in an opportunistic manner when they become available, e.g. temporarily on inundated floodplains.

Natural river corridors and floodplains are disturbance-dominated systems and are recognized as areas of physical, chemical and biological interactions between aquatic and terrestrial habitats resulting in a high diversity of environmental processes (Ward et al. 2002, Strayer & Findlay 2010). In river ecosystems, discharge, especially floods and droughts, is a primary source of disturbance (Puckridge et al. 1998), which varies in its effects on different fish species and age groups (Detenbeck et al. 1992). On the one hand, large floodplains inundated by high floods serve as important feeding areas for fish and nurseries for juveniles (Welcomme 1979, Grossman et al. 1998, Jungwirth et al. 2000, Schiemer et al. 2001b), while on the other hand fish larvae and juveniles may become washed out because of their low swimming performance (Harvey 1987, Pearsons et al. 1992, Bischoff & Wolter 2001). Similarly, droughts may favour fish species that reproduce during low flow conditions (Humphries et al. 1999), although the most frequently demonstrated effects of droughts are declines in populations because higher resource competition and predation occur with increasing concentration in the remaining water volume (Lake 2003, Magoulick & Kobza 2003, Matthews & Marsh-Matthews 2003). Amplitudes of droughts or floods are inversely related to their frequency and thus, significant disturbances are rather infrequent (Reice et al. 1990, Puckridge et al. 1998). However, river fish have evolved several life cycle adaptations to improve their resilience against stochastic environmental disturbances. Such adaptations include high fecundity, multiple batch-spawning, a protracted annual spawning season up to several months, and long life-time fecundity with multi-cyclic (iteroparous) spawning (e.g. Matthews 1998, Jungwirth et al. 2003). Since at least parts of the offspring will approach suitable growth conditions, different species will more benefit from environmental conditions in one year, others in other years and even the complete loss of one cohort can be compensated in the following years (e.g. Figure 4), altogether making populations resilient against environmental stochasticity, as shown for water temperature in Spring by Wolter (2007).

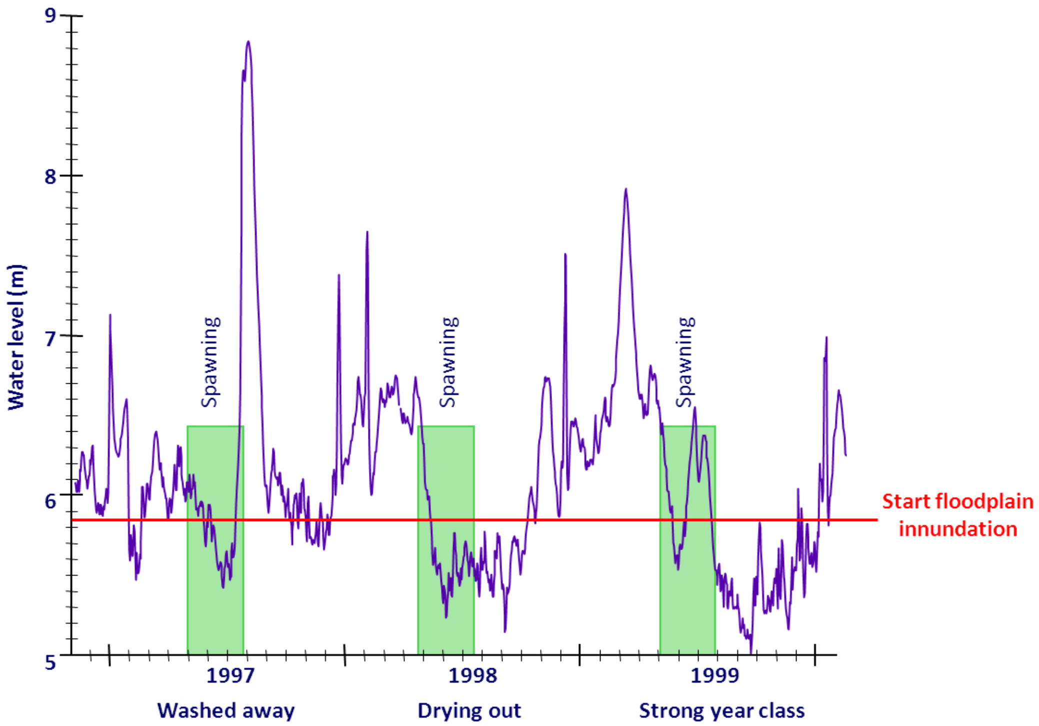


Figure 4 - Recruitment success of silver bream Blicca bjoerkna in relation to water level fluctuations in the lower River Oder in three consecutive years (data from Bischoff 2002).

In time the resilience capacity of river fish assemblages to tolerate disturbances without collapsing is principally mediated by the previously-mentioned high environmental plasticity of river fishes that has evolved in disturbance dominated ecosystems, and which ensures that there is always a minimum of recruitment to sustain population and species survival (e.g. Saunders & Shom 1985). For example even the mostly mono-cyclic (semelparous) Atlantic salmon *Salmo salar* display a wide variability in life-history characteristics, freshwater residence and sea-age at maturity providing resilience against environmental disturbances (Saunders & Shom 1985, Klemetsen et al. 2003). Juveniles become smolts and leave freshwaters in response to environmental cues mostly after one year and often after 2-4 years (McCormick et al. 1998), but they may stay in freshwaters up to 8 years (Metcalfe 1998). Thereby, individual rivers often produce three or more age-classes of smolts (Metcalfe 1998). In addition, adults spend up to 5 but commonly 1-3 winters at sea before reaching maturity (reviewed by Klemetsen et al. 2003). The extremes reported here might total 13 years (8 year old smolt spending another 5 years at sea) which provides a robust capacity to buffer unsuitable environmental conditions.

While salmon can delay their migration to wait for more suitable conditions, most other species gain resilience against environmental fluctuations by multi-cyclic spawning over several, up to ten, years (e.g. Jakobsen et al. 2009). In addition, the annual spawning season of typical riverine fishes is commonly protracted. For example common bream *Abramis brama* and silver bream *Blicca bjoerkna,* both guiding species of the so-called bream zone of floodplain rivers, were observed repeatedly spawning over two and three months, respectively (Poncin et al. 1996, Molls 1997, Harabawy 2002, Figure 4). Typical species of the rivers' so-called barbel region, chub *Leuciscus cephalus* and barbel *Barbus barbus,* commonly spawn for up to six and seven months, respectively (Poncin 1989, Freyhof 1998, Fredrich et al. 2003). In the upper Brazos River, Texas, spawning of sharpnose shiner *Notropis oxyrhynchus* occurred over a six-month period during which individual fish spawn multiple times (Durham & Wilde 2014). Even brown trout, *Salmo trutta,* was found spawning for up to 72 days in Alpine headwaters (Riedl & Peter 2013).

In summary, migratory fish use the whole spectrum of spatial scales up to the catchment, region and even beyond as a migration corridor. Within freshwaters they migrate up to the headwaters (reach scale) where they depend on the availability of suitable spawning gravel, corresponding to specific geomorphic / hydraulic units (Figure 5). Non-migratory species move within the scale of the segment and have their home range within the river reach, where they depend on a certain habitat complexity and heterogeneity formed by patterns of different geomorphic and hydraulic units. The life expectancy of river fishes is well within the typical turnover time of river reaches. As comparably long-living organisms they are able to compensate habitat shifts and disturbances at the scale of geomorphic units and below (Figure 5).

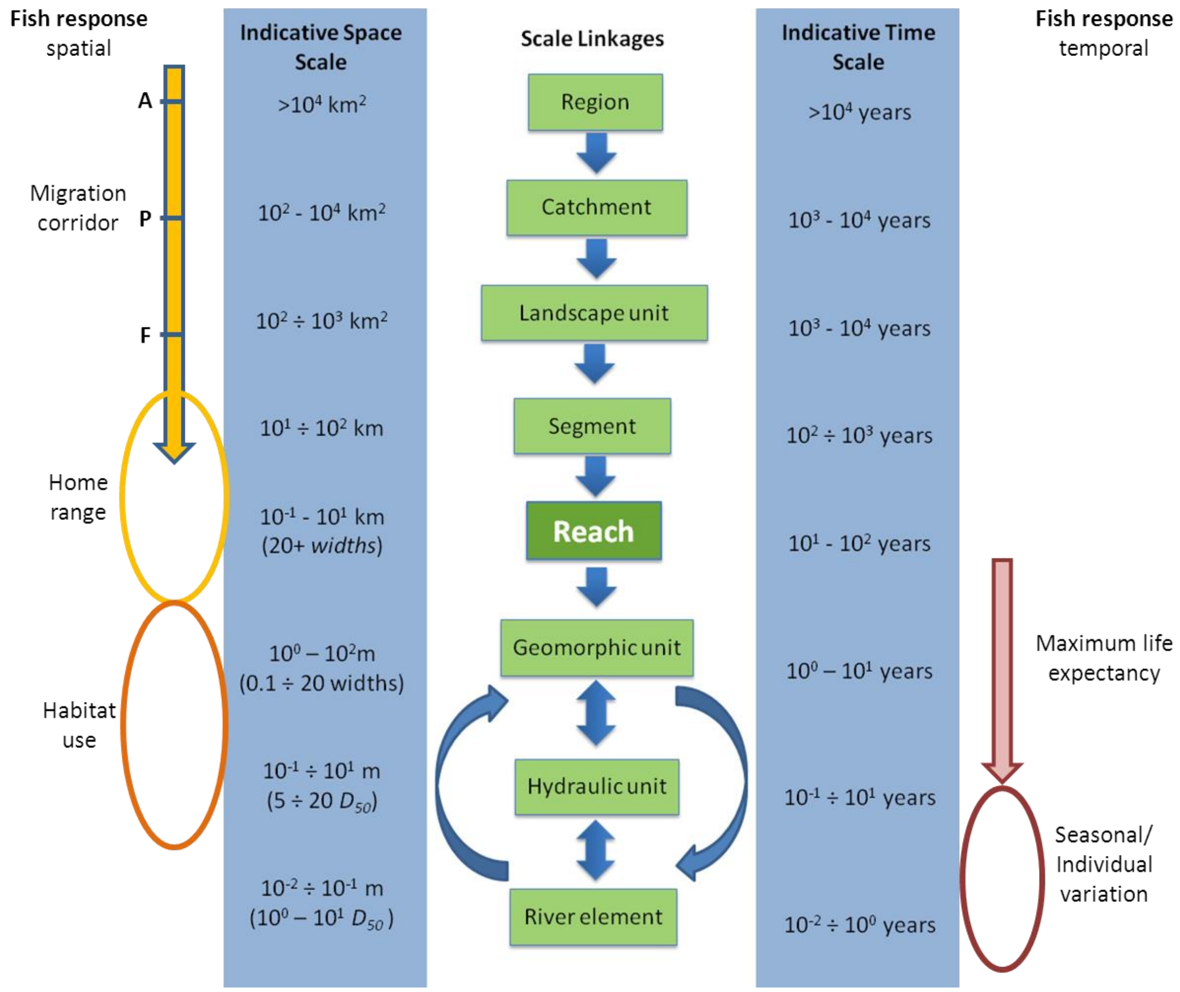


Figure 5 - Correspondence between life cycles of riverine fishes and the natural river typology (A= anadromous/diadromous, P= potamodromous, F= facultative migrants).

4.2.2 Relevant environmental factors at the scale of the different spatial units

Region (>10^4 km²)

Regional faunas are typically evolved along climatic, biogeographic and historic trajectories by natural dispersal and adaptation. For example the freshwater ecoregions of the World (FEOW) provide new global biogeographic regionalization of the Earth's freshwater biodiversity (Abell et al. 2008, http://www.feow.org/). Stressors acting at this spatial scale include global climate change but also migration barriers. Diadromous fish depend on migration pathways at this large spatial scale and become strongly impacted, including their total disappearance, if the connection between marine and freshwater habitats is blocked. A region or FEOW typically contains several catchments, e.g. 16 of the European FEOW contain more than five catchments larger than 2500 km² each. River systems within one FEOW share a high similarity in their fish communities, so that blocking migratory species from single catchments does not inevitably cause their disappearance from the whole FEOW.

Catchment (10^2 – 10^4 km²)

Fish species inventory of catchments is commonly determined by the regional biogeography (Lamouroux et al. 2002, Oberdorff et al. 2011) and at the present time also by human-mediated spread of non-native species (Rahel 2007, Villéger et al. 2011). The number of species within catchments strongly positively correlates with drainage area (e.g. Oberdorff et al. 1995, 2011), and habitat heterogeneity (Guégan et al. 1998, Oberdorff et al. 2011). Accordingly, European catchments larger than 2500 km² receive between 7 and 132 lamprey and fish species, with an average of 39 (Sommerwerk, unpublished). In 1054 river basins world-wide, an inventory of lampreys and fishes yielded between 1 and 1802 species per catchment, in Tropical and Oriental realms on average 60, in the Nearctic 38, in the Palaearctic 25, and in the Australian realm 17 (Lévèque et al. 2008, Brosse et al. 2013). Beside the global pressures and stressors mentioned above, land use and land use change become relevant impacts at this spatial scale. Certain land uses, especially intense agriculture, serve as diffuse source of nutrients and fine sediments leading to water quality changes and siltation of the interstices between river bed particles. Substantial eutrophication and loads of fines typically result in the loss of sensitive species with high oxygen demands. At the catchment scale migration barriers affect larger numbers of obligatory migratory species, both diadromous and potamodromous. However, comparable to the region effects, fish are linked to their spatial requirements for migration pathways.

Landscape unit (10^2 – 10^3 km²)

At the smaller scale of the landscape unit the effect of migration barriers becomes more pronounced because dispersal and movements of facultative, i.e. non-obligatory migrants become affected too. At the level of landscape unit, river fragmentation by barriers is already reflected in a limited genetic exchange. Other stressors like climate and land use change act on the fish community as a whole in a similar manner to the higher spatial scales, because the average turnover time at the landscape level is far beyond the life span of fish.

At the spatial level of landscape units hydromorphological changes other than barriers and dams become relevant, especially in navigable large rivers. Over most of their main channel length, they had been typically regulated, and modified to single-thread channels with depth- and width-homogenised fairway , steep bank slopes and heavy embankments to prevent lateral erosion. This hydromorphological degradation results in significantly reduced water retention, higher flow velocities in downstream river sections, incised channels, floodplain dewatering and a large scale loss of slow flowing, shallow, littoral habitats.

Segment (10^1 – 10^2 km)

At the spatial level of segments fragmentation of rivers by barriers potentially impacts all fish species by blocking all movements over longer distances, including compensation and dispersal movements. Secondary effects of barriers, such as impoundments, are reduced stream power, interrupted sediment transport, and reduced availability of hydromorphological habitat structures may start to become relevant at this level. However, many of the other stressors mentioned above still act on the fish community as a whole, because the average turnover time even at the level of segments is beyond the life span of fish.

In particular, in larger rivers the segment scale commonly corresponds to the scale of functional process zones *sensu* Thorp et al. (2006), i.e. to the fish regions. Fragmentation within a fish region might prevent utilisation of essential habitats by type-specific species, modification of flow regime and stream power by barriers and river engineering might cause the loss of essential habitats, and finally, the remaining river fragments might become too small to serve a healthy, abundant fish population.

While the general decrease of typical riverine, rheophilic fish due to large scale habitat loss and modifications has been well documented, there is so far no quantitative relation available for the decline of fish due to habitat loss. By comparing the fish assemblages of different lowland waterways in Germany, Wolter & Vilcinskas (1997) found an inverse relation of fish diversity and abundance and artificial embankments. An additional steep and significant further decline in species numbers and the abundance of sensitive fish was detected if the total amount of embankments of a waterway exceeded 80% (Wolter & Vilcinskas 1997, Wolter 2001).

Reach (10^{-1} – 10^1 km, 20+ river widths)

The reach scale seems the most relevant scale for fish communities, because individuals typically respond at this spatial and temporal scale. The river reach utilised by individuals over a season is rather small, except for spawning migrations (Radinger & Wolter 2013). By reviewing and analysing 160 empirical datasets from 71 studies covering 62 fishes in streams, Radinger & Wolter (2013) confirmed the concept of heterogeneous movement (Skalski & Gilliam 2000, Rodríguez 2002) and determined a median movement distance of the stationary and mobile component of a fish population of 36.4 m and 361.7 m, respectively. These distances differed between taxonomic families (Figure 6) but they are always both well within the spatial scale of the river reach. The share of the stationary individuals was high (median = 66.6 %) but unrelated to movement distance.

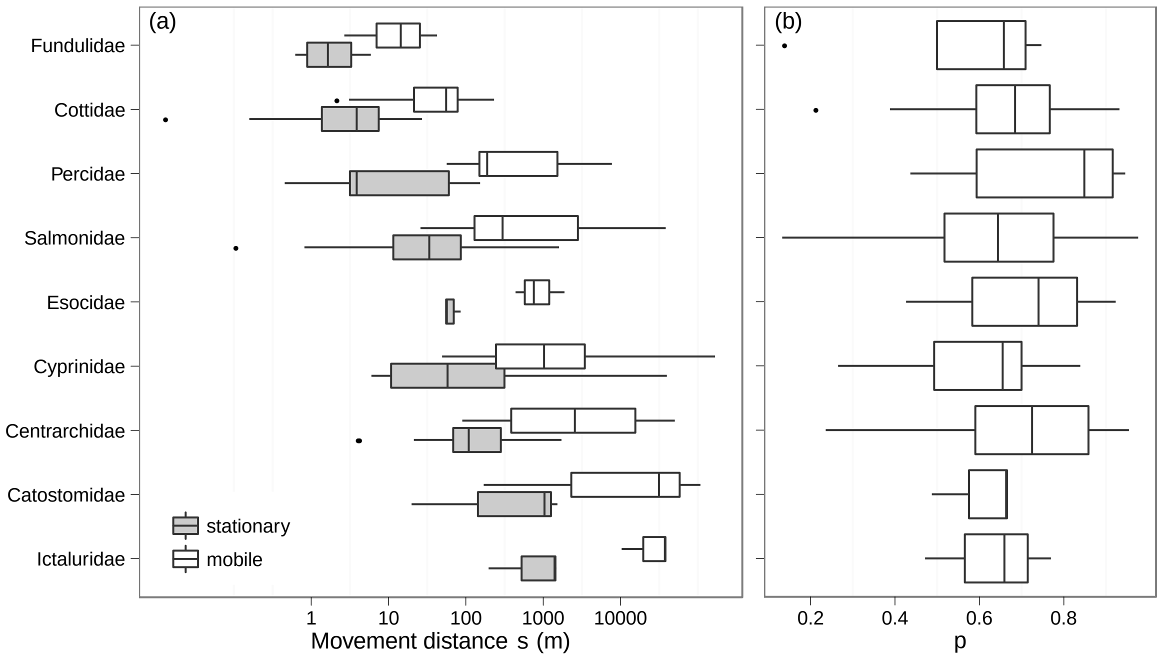


Figure 6 - Characteristics of movement parameters across taxonomic families (n > 2): (a) Movement distance σ of the stationary (grey boxes) and mobile (white boxes) component. (b) Share of the stationary component (p) (from Radinger & Wolter 2013)

The river reach is comprised of geomorphic and hydraulic units and river elements such as boulders, bars, pools, large wood, variability in depth and width, heterogeneity of flow velocity and physical habitats, aquatic macrophytes, and riparian cover. These complex habitat and flow velocity patterns and their interplay form functional process zones according to Thorp et al. (2006) with ecological communities controlled by the hydrogeomorphic patches ensemble at the reach scale. River systems provide a hierarchical, longitudinal array of reaches, i.e. 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 empirically derived concept of fish regions to characterize the longitudinal zonation of rivers has been used for more than 100 years (reviewed in Wolter et al. 2013). The probability of fish species occuring in a certain river region corresponds to how the ecological requirements of a species are supported by the typical geomorphic and hydrodynamic settings within the reach as well as the ability of the species to withstand the typical frequency and magnitude of disturbances (Figure 7). Therefore, the species' preference for a functional reach reflected by its longitudinal distribution is an important indicative feature for ecological integrity at the reach scale (e.g. Grenouillet et al. 2004). This approach is still in use for fish-based assessments in Austria and Germany (Schmutz et al. 2000, Dußling et al. 2004, 2005) and has been adopted and harmonized within REFORM (Wolter et al. 2013).

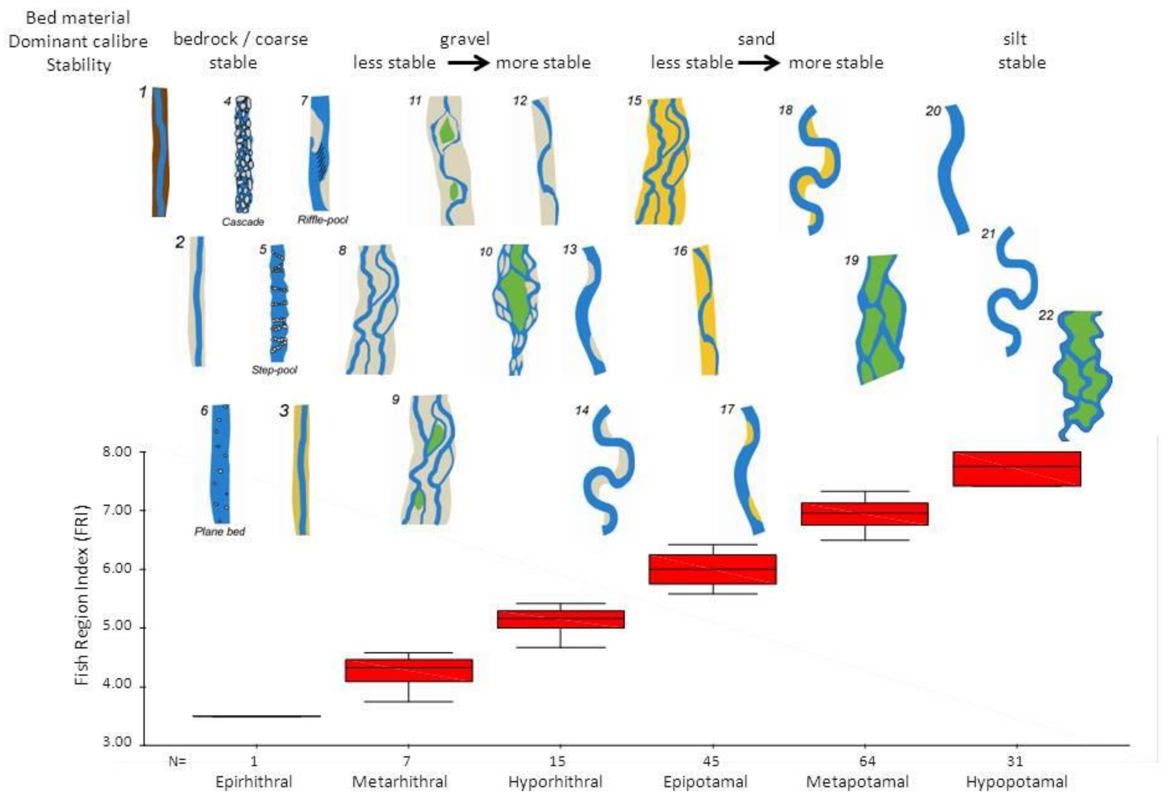


Figure 7 - Approximate correspondence between river types and species-specific Fish Region Index; N= number of species, classification according to Wolter et al. (2013).

Human impacts at the reach scale comprise river regulation, channelization, damming, cutting off floodplains, and other morphologic alterations, as well as impacts at larger spatial scales from the catchment upstream, e.g. nutrients, fine sediments, or temperature. Morphological alterations typically change the character of a reach by homogenising and simplifying habitat patterns or geomorphic units, by rhitralisation or potamalisation. Changes in the hydromorphological character of a reach will result in changes of its fish assemblage which becomes measurable by significant changes of the newly harmonized Fish Region Index (Wolter et al. 2013). This metric still allows for assessing hydromorphological degradation and rehabilitation of river reaches based on fish.

At the reach scale the loss of lateral connectivity and availability of floodplain areas is highly relevant. Inundated floodplains provide important feeding areas for fish, spawning habitats and nurseries for juveniles (Welcomme 1979, Grossman et al. 1998, Jungwirth et al. 2000, Schiemer et al. 2001b, Harabawy 2002, Grift et al. 2006). Floodplains are also a significant element of the resilience against flood disturbances that has evolved in riverine fish. Inundated riparian and terrestrial vegetation mitigate the impact on fish by stream power at high floods by providing shelter and refuges (Pearsons et al. 1992).

Geomorphic unit (10^0 – 10^2 m)

The geomorphic unit corresponds to the micro- and meso-habitat level commonly studied to determine preferences of juvenile fish (e.g. Copp 1992, Scheidegger & Bain 1995, Freyhof 1998, Jurajda 1999, Grift 2001, Schiemer et al. 2003, Scholten 2013). Numerous geomorphic units have been described as micro- or meso-habitats for fish. However, the latter often use and respond to different geomorphic units in a more general way (Table 4), i.e. there is rarely a specific association between diagnostic species / age groups and specific geomorphic units. Further, fish typically require an ensemble of different geomorphological units at larger spatial scales, commonly at the reach scale (Figure 8).

Table 4 - The Geomorphic Units differentiated within the present river typology and their potential use by fish.

Geomorphic unit	Sub-type	Fish-ecological relevance / fish use
Cascade / Rapid		Adult fish, migratory fish
Step (-pool)		Adult fish, resting, shelter
Riffle		Adult lithophils, spawning, Lithophilic species egg development, hatch and larvae growth, feeding
Pool		Juvenile and adult fish, shelter, feeding
Ripple		Adult fish feeding, psammophilic fish spawning, egg development
Dune		Adult fish feeding, psammophilic fish spawning, egg development
Mid Channel Bar	Longitudinal bar	Juvenile fish, small-bodied adults, shelter, feeding, low-flow refuges
	Transverse bar	Lithophilic fish, spawning (depending on gravel size), juvenile fish, shelter, feeding
	Diagonal bar	Juvenile fish, small-bodied adults, shelter, feeding, low-flow refuges; lithophils spawning
	Medial bar	Juvenile fish, small-bodied adults, shelter, feeding, low-flow refuges
Island		Adults, juveniles, small bodied species, refuge, shelter, feeding
Marginal Bar	Lateral bar Point bar Scroll bar	Juvenile fish, small-bodied adults, shelter, feeding, low-flow refuges
Wood dam/jam	Simple Bench jam Flow deflection jam Bar apex jam Valley jam Meander jam Counterpoint jam	Adults, juveniles, all species, shelter, refuge, resting sites, feeding area, creates flow diversity, local sediment sorting, sand and gravel patches for spawning, protection from high stream power
Forced pools, bars, riffles		Adults, juveniles, all species, shelter, refuge, feeding
Pioneer island		Juvenile fish, small-bodied adults, shelter, feeding, low-flow refuges
Vegetation-induced bars, benches, islands	Chute channel Counterpoint bar	Adult fish, shelter, cover, feeding sites, spawning sites for phytophilic and phyto-lithophilic fish; juvenile fish and subadults, shelter, feeding
Berm / bench		Adult fish, feeding

Geomorphic unit	Sub-type	Fish-ecological relevance / fish use
Alluvial fan		Adult fish, temporary spawning for phytophilic and phyto-lithophilic fish, juveniles and adults temporary feeding site, refuge from high stream power
Terrace		Adults, juveniles, spawning, feeding on inundated terraces
Abandoned channel (lake, wetland)		Limnophilic and eurytopic fish, phytophilic spawners, adults, subadults and juveniles
Oxbow (lake, wetland)		Limnophilic and eurytopic fish, phytophilic spawners, adults, subadults and juveniles
Back swamp		Limnophilic fish, floodplain specialists

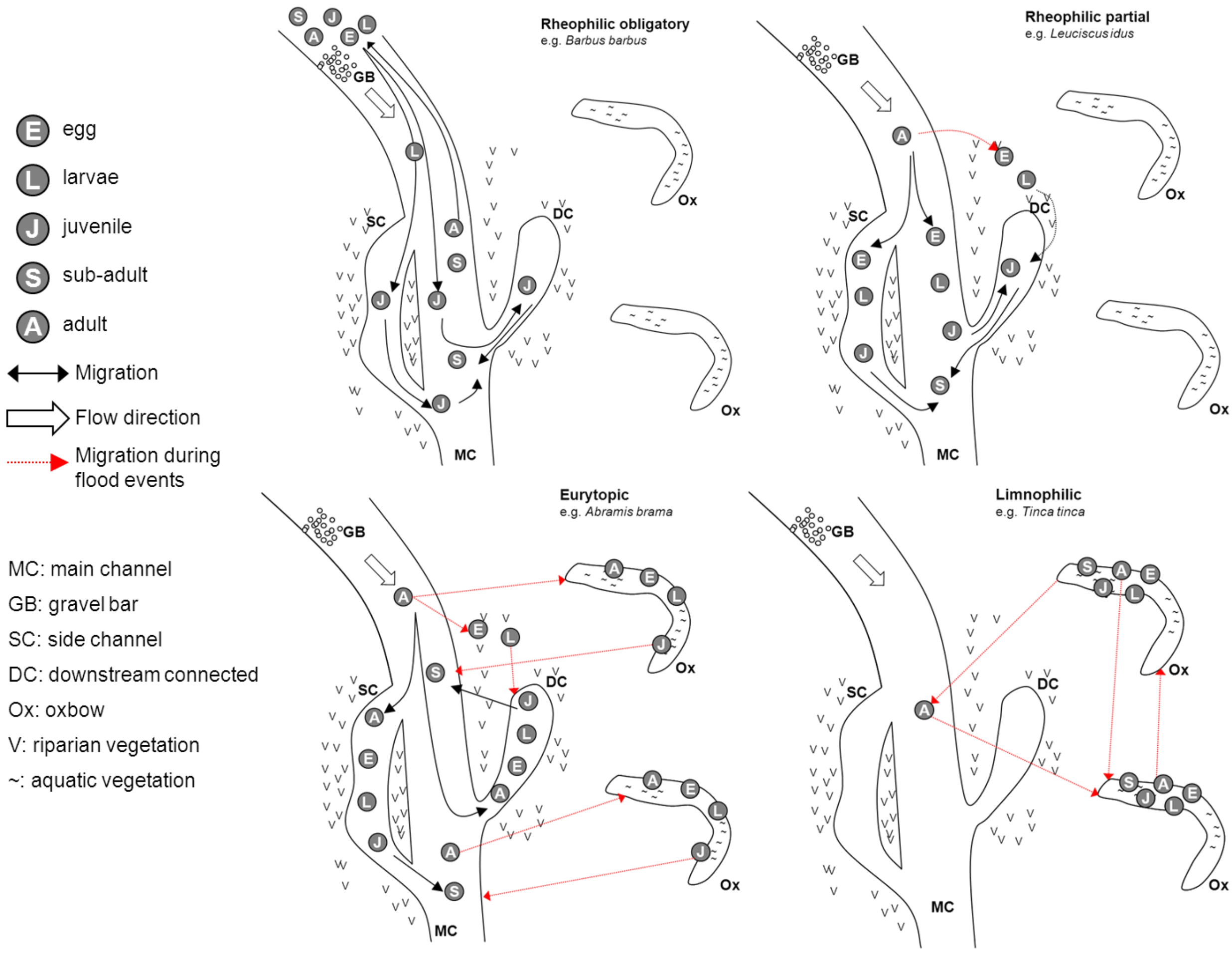


Figure 8 - Temporary use of geomorphic units by different life stages of major ecological guilds of riverine fishes (modified from Grift 2001).

For hydromorphological features and structures as well as river rehabilitation it has been conceptualized by Wolter et al. (2013) that gravel bars represent a significant, geomorphic unit indicative of highly specific interactions between hydromorphology and both rheophilic and lithophilic fish. 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, indicators for hydromorphological integrity. Accordingly, specific indicator taxa for hydromorphological alterations should respond to these specific substrates, especially to coarse gravel. In contrast to the more general response of fish to other geomorphic units (compare Table 4), obligatory gravel spawning is a life history trait which is directly and strongly connected to coarse well oxygenated sediments, corresponding to gravel bars as the geomorphic unit. In their response to gravel provision, species differ in their requirements for gravel calibre, gravel sorting, bar permeability, and amount of tolerated interstitial fines (reviewed by Wolter et al. 2013).

Fish species express further preferences, e.g. for large wood as cover or shelter as well obligatory requirements e.g. of plant spawners for aquatic macrophytes or inundated terrestrial vegetation. Other significant geomorphic units like submerged and emergent macrophytes in low energy and floodplain rivers and large wood in high energy rivers provide shelter, refuges and feeding grounds or spawning substrate for plant spawners. They are similarly essential to sustain a species-rich diverse fish assemblage; however, there is no quantitative relation available to conclude from species presence or abundance on the amount or availability of such structures. In contrast, a well age structured population of lithophilic fish indicates that there is suitable spawning substrate available at least somewhere in the reach which is at least sometimes connected.

Hydraulic unit (10^{-1} – 10^{1} m)

Hydraulic conditions in general determine the connectivity between and availability of the various habitats and habitat structures for fish. Hydraulic units are relevant in two ways. On the one hand they connected to geomorphic units because a relatively homogeneous surface flow structures a certain substrate calibre that for gravel bars especially influences the permeability and thus, the oxygen supply for eggs and larvae of gravel spawning fish.

On the other hand low energy hydraulic units, i.e. zones of low and very low flow velocities are essential for the natural recruitment of nearly all fish species. Being weak swimmers, fish larvae and small juveniles essentially depend on the availability of low flow zones. The amount of low-transit zones controls the downstream displacement of fish and determines the availability of nursing habitats (Wolter & Sukhodolov 2008, Sukhodolov et al. 2009) and thus determines the carrying capacity and the recruitment potential of larger spatial units.

The availability and amount of low-transit zones can be modelled from geomorphic units up to reaches (Wolter & Sukhodolov 2008, Sukhodolov et al. 2009) and the carrying capacity for offspring calculated accordingly. However, the species composition of the juvenile assemblage is determined by the adult spawning stock and the availability of suitable spawning substrates i.e. of the relevant geomorphic units.

River element (10^{-1} – 10^{-2} m)

River elements are of such a small spatial extend and high turnover rate that they cannot be separated from individual behaviours, movements, plasticity within fish assemblages and populations. Fish indirectly respond to river elements at the level of hydraulic or geomorphic units.

5. Floods and droughts as biota-shaping phenomena

This chapter again considers the hierarchical time and space framework proposed in deliverable 2.1, but with an emphasis on extreme flow events. The objective is to investigate the response of fish and invertebrate communities to these events as they occur in natural systems (i.e. without man-made alterations). The influence on flora has been discussed in chapters 2.2.3-2.2.5 of Part 1.

5.1 The role of extreme hydrological events

5.1.1 Introduction

In an ecological sense floods and droughts are considered physical disturbance events, i.e. stochastic events forcing normal system environmental conditions substantially away from the mean (Stanford and Ward 1983). The disturbance has been very intensively studied and debated among stream ecologist (Stanley et al 2010). It is considered a significant ecological phenomenon that could alter biotic interactions (Hemphill and Cooper 1983, McAuliffe 1984, Power et al. 1985) and community composition in streams (Fisher et al. 1982, Grossman et al. 1982, Reice 1985). Physical disturbance is a natural component of aquatic ecosystems (Resh et al., 1988; Fisher & Grimm, 1991; Poff, 1992; Lake, 2000, 2003) and can be a major factor in structuring aquatic communities (Fisher et al., 1982; Resh et al., 1988; Poff & Allan, 1995). Lotic community structure can be strongly influenced by physical disturbance, such as floods and droughts (Resh et al., 1988), but lentic communities can also be affected (Freeman & Freeman, 1985). A key ecological element of physical disturbance is availability of refuge that assures the survival of aquatic populations (Lake 2000, Magoulick and Kobza 2003 Figure 10). In many cases, although ecological processes or populations will be different during a flood or drought, the system returns to normal once the event is over; i.e. the system recovers. In such cases the event has no long term implication for the ecosystem. It is important to distintinguish this from extreme events during which thresholds are crossed such that the ecosystem moves to a different state (that may be stable or unstable). In this cases the events are important in terms of long term ecological change.

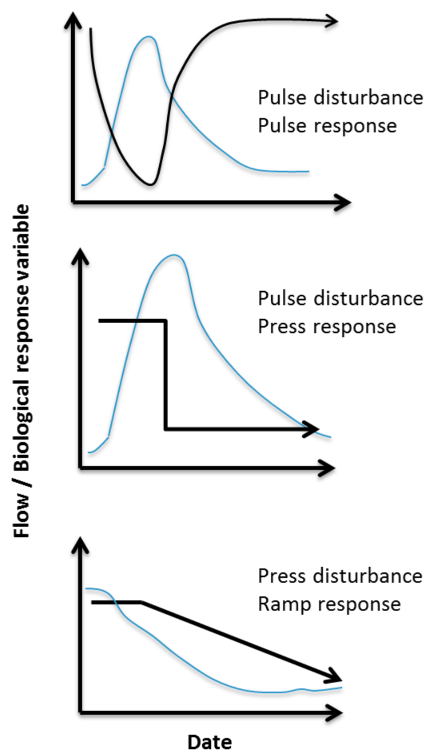


Figure 9 - -A concept of disturbance types using example of flood (top two) and drought (bottom). Modified from Lake 2000. Blue lines represent riverflow.

There are three types of disturbance: pulse, press and ramp, which trigger three different processes that alter populations. A pulse disturbance causes an instantaneous alteration in fish or invertebrate densities, while a press disturbance causes a sustained alteration of species composition. Ramps have been defined as disturbances that increase in strength (and often spatial extent) with time (Lake, 2000 Figure 9). Obviously these definitions refer to a time scale comprehended by individual organisms, and for aquatic fauna the spacial scale of reach. At this scale floods are most often pulse or press disturbances, and droughts tend to be more of the ramp kind. At coarser temporar scales all disturbances may turn into pulses.

Figure 10 - Refuge available during drought of 2007 on the Fenton River, CT

The processes triggered by floods or droughts can create two types of changes: concurrent i.e. occurring only during the event; and post-event changes that remain after the event for a considerable time. There are two generally recognized forms of biological response to disturbance: resistance (the capacity of the biota to withstand the disturbance); and resilience (the capacity to recover from the disturbance) (Lake 2000). The third type of response is opportunistic utilization of habitats that are created by the disturbance e.g. spawning or predation habitats (e.g. Grift et al 2001, Welcomme 1979). The resistance concurrently with the evens and resilience is rather post disturbance phenomenon. Opportunizm can be observed in both phases. Figure 11 represents this concept on the example of floods.

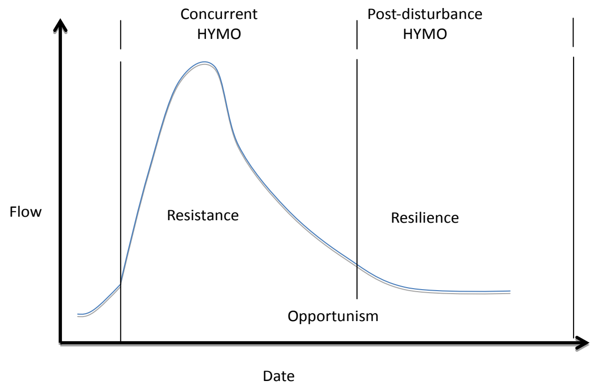


Figure 11 – A concept of HYMO changes and biological response types during the flood event. Blue line represents flow in the river

5.1.2 Hydromorphological consequences of floods and droughts

According to the theory of habitat templates the structure and size of aquatic populations is shaped by availability their habitat (e.g. Poff and Ward 1990). This is not constant, but changes over time and is to a large extent due to change in HYMO patterns. Extreme floods and droughts have a tendency to reduce or expand the habitats into the terrestrial zones and therefore frequently serve as ecosystem shaping events, which may cause long lasting imprints on the structure and condition of aquatic fauna (e.g. Arthington et al 2005, Peterson and Kwak 1999). For fish, as a consequence of their long life span, the catastrophic impacts of one event (e.g. depleting of one generation) may propagate well into following years (e.g. Cowx et al 1984).

In order to better understand the influence of extreme events on biota we have to analyze the nature and mechanisms of habitat change occurring during such events. This may allow the isolation of causal relationships between HYMO and biology and to estimate the intensity of impact as a function of event characteristics. Therefore in the first part of this chapter we focus on described HYMO changes occurring during extreme hydrological events that may cause biological consequences, and later we describe the biological response.

Floods

In hydrological terms, floods are natural events occurring periodically within the expected range of streamflow (Smith & Ward, 1998). These events result from moderate to large phenomena of precipitation or high tides causing exceedance of the threshold discharge (Strupczewski, 1966; Ozga-Zielinska, 1987). Some floods have high predictability and show seasonal frequency (e.g. long durational flood pulses) meanwhile others are more unpredictable (e.g. flash floods, extreme in the case of hurricanes). Historically the flooding threshold was defined as the mean of annual maximum flow from an N-year record. More recently bankfull flow has been considered as a more adequate flood disturbance threshold (Poff 1992, Richards 1982). Bankfull flows are discharges with that correspond to the highest stream power within the channel (frequently causing channel forming processes). At flows higher than bankfull river flows out of its typical channel into the floodplain. As documented by Schwartz and Herricks (2011), fish habitat use also changes at flows higher than bankfull towards utilization of flow refuges (i.e. areas of slow velocities in the floodplain), further underscoring the significance of this threshold. This happens in response to the physical changes that take place.

Concurrent changes

At the onset of a natural flood event the increasing discharge raises the flow velocities, and the thallweg part of the river channel deepens and widens. The nature and distribution of hydromorphologic units such as riffles, pools or runs changes towards dominance of the run type of habitat (Leopold et al 1992, Figure 12).

River Confluence Arga-Aragón during January 15th 2010 flood

Figure 12- Flood on the confluence of Aragon and Arga Rivers in Spain (Photo. D.G. de Jalon)

Hence, the flow pattern becomes dominated by velocities that in the main channel may exceed swimming capacities of most of the fish species. New areas of normally dry channel banks and floodplains become inundated and linked to the river, providing refuge habitat of slower velocity. The fast thalweg and slow lateral areas are separated by distinct hydraulic boundaries (Schwartz and Herricks 2005). Due to the velocity-reversal phenomenon, mobilization and deposition patterns reverse: pools are scoured and deposition takes place at the riffle areas (Keller and Florsheim 1993, Thompson et al 1999), with little difference in water depth and velocity between pools and riffles (Hogan & Church, 1989). Fine particles are moved into suspension, dramatically increasing water turbidity, and they are deposited in different areas during flooding, particularly the floodplain during overbank floods. Nutrients deposited in the floodplain are also mobilized, further affecting water quality (Edwards et al 2012). Water temperature also frequently changes. Generally, it can increase (e.g. in consequence of warm thunderstorms) or a decrease (e.g. snowmelt waters), but also becomes much more diverse in a cross sectional profile (Tockner et al 2000). Overall we can conclude that although the wetted area dramatically increases, particularly during large over-bank events, it becomes in uninhabitable in some parts due to above changes, although some parts remain as hydraulic refugia. The extent of refugia is a function of river type and morphology (eg. Tockner et al 2000) . Large low gradient rivers inundating extensive floodplains create vast areas in former terrestrial zone that can be utilized by fish, while constrained, high gradient streams mainly offer velocity shelter within the channels (Bunn et al 2006, Hickey & Salas 1995).

Morphological changes induced by floods can differ according to valley confinement and river typology. In constrained rivers, usually with a coarse substratum forming cascades or step-pools, floods increase flow velocity and shear stress, creating major changes in channel morphology by scouring and filling the streambed (Gordon et al., 2004). In lowland rivers with extensive floodplains, flood energy is more easily dissipated and water velocity and shear stress may not increase significantly (Figure 13). In this case floods inundate the floodplain and deposit sediments and organic particles, filling wetlands, anabranches or flood runners with a slow moving flow which recedes slowly, and is transformed from being a damaging disturbance to a major regenerator of biodiversity and production disturbance (Lake, 2007).

Figure 13 - Flooding of lowland Biebrza River in Poland (photo: T.Okruszko).

Post disturbance effects

In the longer term, floods reshape the distribution and composition of habitat. The substrate, as well as water depth and velocity distribution occurring during low flows may become very different. Large quantities of debris (frequently dead wood) create new hydraulic conditions and food availability. Obstacles such as wood jams are removed or relocated. The consequences may range from spatial rearrangement of habitats, while maintaining a similar quantitative distribution, to complete destruction of habitat for some species and creation of habitats for others (Arthington et al 2005, Roghair et al 2002). This may not only be due to morphological but also to biological changes (see below). In some cases the morphology of the channel returns to pre-flood conditions (dynamic equalibirum) but this depends on lower flows being competent to move sediments, so recovery is partly determined by river and sediment type.

The overall effect of a flood is related to its duration, magnitude, frequency and predictability combined with consideration of elements of the stream's substrate composition, stability, refugia, and natural flow regime (Poff, 1997, Lake, 2000, Lake, 2007). However, as floods are pulse disturbances, their effects are most strongly related to the magnitude of the event (Molles, 1985; Grimm and Fisher, 1989). Hence the effects of flooding may vary from small spates or freshets causing little geomorphological change, to extended, powerful high discharge events that can alter the structure of the stream channel entirely (Costa & O'Connor, 1995). Wolman and Miller (1960) showed that flows of bankfull discharge do the most geomorphological work because they have significant stream power and occur relatively frequently. Unseasonal floods are acknowledged to be more damaging than those that occur during typical wet seasons (Lytle, 2003, Giller, 2005).

Droughts

Drought is a condition of insufficient water availability caused by a deficit in precipitation over an extended time period (Mckee et al 1993). Hence they are defined by the amount of water and duration of low flows. Therefore drought is considered a "creeping phenomenon" whose beginning and current status are difficult to define (Grigg 1996, Whilite and Glanz 2009). Defining drought hydrologically is problematic because the return times, intensity, duration and long-term trends in low-flow periods are specific to regions and times (Humpreys and Baldwin 2003). One option is a retrospective investigation of negative-run-time lengths of the flow time series with the help of Uniform Continuous Under Threshold Curves (Parasiewicz et al 2013. Figure 14). This technique allows one to identify drought thresholds based on the historical frequency of occurrence of rare events. Droughts can be divided into those that cause predictable, seasonal press disturbances and less predictable, protracted 'ramp' disturbances (Humpreys and Baldwin 2003). Droughts can either be periodic, seasonal or supra-seasonal events. Seasonal droughts are press disturbances, whereas supra-seasonal droughts are ramps marked by an extended decline in rainfall (Lake 2003).

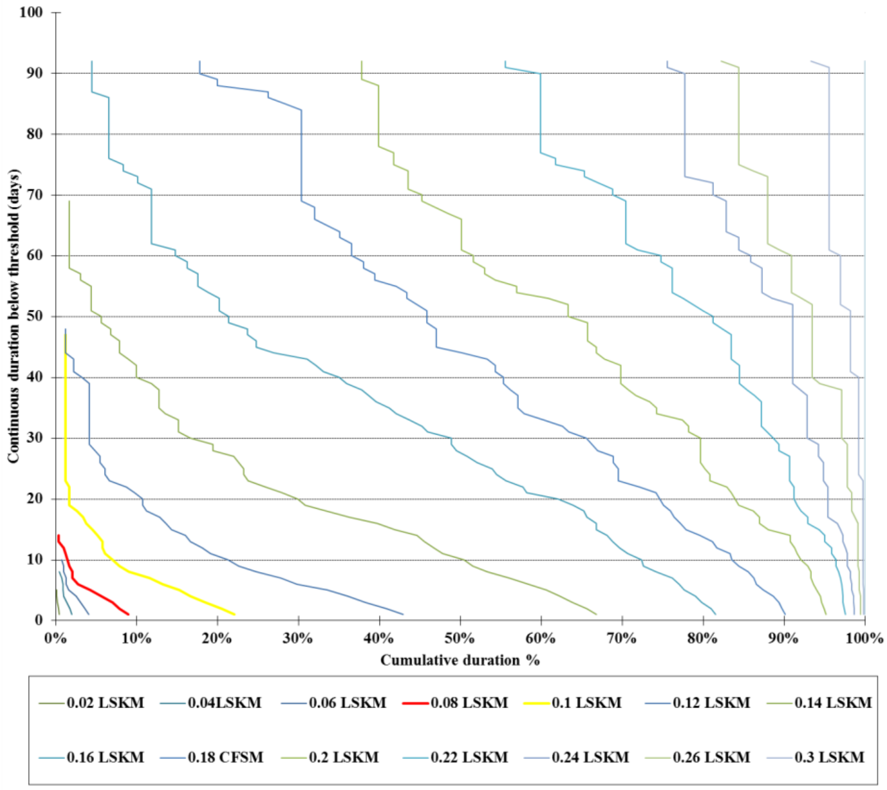


Figure 14 - UCUT curves for specific flows winter (in ls-1km2, LSKM) on Niobrara River (48 years data series). Each curve represents cumulative duration of events when flow was continuously below selected flow level. The curves in the left corner indicate low frequency events and the red one is selected as a drought threshold

Droughts tend to be more spatially extensive than floods, which are frequently limited to individual basins (Edwards et al 2012). Human activities may exacerbate or even introduce drought conditions (Boix et al 2010, Lake 2011 b). Again we can distinguish concurrent and post-disturbance changes.

Concurrent changes

During a drought, precipitation, runoff, soil moisture, groundwater levels and stream flow decline sequentially (Changnon, 1987; Grigg, 1996;Dahm et al., 2003). Similarly to floods, during the drought there are both direct and indirect effects on stream ecosystems. Typically direct effects include loss of water, loss of habitat for aquatic organisms and loss of stream connectivity (Lake 2003, Figure 15).

Figure 15 - Loss of connectivity on the River Rhine in Netherlands in May 2011 (Photo: T. Buijse)

Loss of water results from lack of replenishment from upstream and may be augmented by evaporation and evapotranspiration, or loss of water into the subsurface. The indirect effects include the deterioration of water quality by increased concentration of biogens despite lower input of nutrients (Dewson et al., 2007, Golladay & Battle, 2002, Zielinski et al., 2009). The ratio of inorganic to organic nutrients declines, potentially causing a shift in stream metabolism (Dahm et al 2003). Due to reduced sediment transport capacity the fine particles as well as organic matter are deposited on the surface and in the interstitial spaces (McKenzie-Smith et al., 2006, McMaster & Bond, 2008, Figure 16). An increase in the density of aquatic organisms as well as growth of algae and cyanobacteria feeding on the concentrated nutrients may lead to oxygen depletion and potentially hypoxic conditions (Suren et al., 2003b). During hot periods, a continuous increase of water temperature is accompanied by reduced inflow of cold groundwater and subsequent disappearance of thermal refugia (Elliot 2000, Torgensen et al. 1999). Higher temperature increases decomposition rates and reduces oxygen concentrations due to reduced solubility. During cold weather periods, droughts may lead to lowering of water temperature, ice and frazil ice formations. Frazil ice tends to scour river bottoms causing morphological change (Lake 2003). Overall habitat area and quality declines in association with droughts (Figure 17).

Figure 16 – Entire lake drawdown in Danube Delta during drought in August 2007 (Photo T. Buijse).

Figure 17- Reduction of habitat area during the drought in the Rhine Delta May 2011 (Photo T. Buijse).

Post disturbance effects

The long term changes depend on drought intensity, duration and the ability of the ecosystem to recover. This can be physical recovery in terms of habitat renewal or biological recovery that may be controlled by the ability of organisms to recollonise.. The HYMO consequences of moderate droughts, when the river does not completely dry out, are not as dramatic as after floods. The occurring changes are mostly of a morphological and chemical nature and are consequences of ice introduced scour and sedimentation. Growth of macrophytes and riparian vegetation during droughts can create new morphological patterns after the event. However after drying, the bare ground undergoes important chemical changes, increasing phosphate retention and re-oxidisation of sulphur, that may lead to acidification after re-wetting (Baldwin & Mitchell, 2000, Lamontagne et al., 2006). Sediments also lose their retention capacity and subsequent downpours can cause substantial erosion and mobilization of large amounts of nutrients from riverbed and riparian areas (Edwards et al 2012).

5.1.3 Biological response drivers (what is causing biological response)

Factors that directly trigger biological response include change of habitat area and habitat quality. The physical habitat quality attributes are related to flow velocity, water depth, substrate stability, temperature and water quality as described above. These factors affect biota at the scale at which they perceive their environment (i.e river element and hydraulic unit). Once the factors exceed the suitable range they cause reaction of individuals that is: 1) changes in habitude (adjustment of habitat suitability criteria) 2) search for areas offering refugia (Lancaster and Belyea 1997, Meffe 1984).

Floods

Concurrent response

Floods increase the overall habitat area, although much of this area may become uninhabitable due to high velocities, suspended solids or chemical loads. In such sections biological response is characterized first by change of habitude from, for example, foraging to refuge seeking or spawning. It could be assumed that animals are occupying the same locations by lowering their habitat quality standards (habitude) until specific thresholds of discomfort are exceeded. However, studies have documented benthic macroinvertebrates evacuating the foraging habitats already prior to the arrival of a flood wave and moving into the hyporheos (DoleOlivier et al., 1997, Matthaei et al 1997,) or into pools (Fausch et al., 2002). It is possible that fish may act the same way when floods are predictable utilizing for example tributaries as a refuge. Nevertheless, many species or life stages that are not well adapted to local flooding conditions are displaced by flood waters. This is often the case for juvenile fish and macroinvertebrates unable to find refuge in interstitial spaces or to withstand high flow velocity (Shannon et al 2001). In rivers without floodplains the consequence is reduction of abundance and diversity of macroinvertebrates. This is not necessarily the case for fish. Salmonids for example are well adapted to high velocities and use floods to reach spawning grounds that are not available and suitable during lower flow conditions (DeVries, 1997). Many species use the flood wave as a dispersal mechanisms for their eggs e.g Australian grayling (O'Connor and Koehn 2006); silvery minnow (Platania and Altenbach 1998) and spawning takes place on the rising limb of the hydrograph (Welcomme 1979). Nevertheless, extreme events may scour the eggs or sediment deposits and may prevent the emergence (Carline & McCullough, 2003, Cowx & de Jong, 2004, Phillips et al., 1975). Adult fish may also be affected by displacement and injury caused by moving debris and bed instability, or shortage of food (Jensen & Johnsen, 1999, Lusk et al., 1998, Weng et al., 2001).

By expansion to the terrestrial zones of low gradient rivers, however, there is a net increase of habitat area, which offers refuge and foraging habitat. The additional influx of nutrients supports rapidly growing populations of macroinvertebrates (Hickey and Salas, 1995). This creates an abundance of prey for fish (Allen, 1993, Junk et al., 1989). The abundance of phytophilous and phytolithophilous species increases due to better food and shelter availability (Jurajda et al 2004). However, such a situation is rather rare during winter floods. In high gradient rivers, floods offer an opportunity to pass normally unpassable barriers allowing for access to upstream habitats, fact used for many species to access spawning grounds in tributaries.

Many species have evolved life cycles that depend on floods for spawning, nursery and foraging habitat. The most well-known example is spawning salmonids, which migrate into tributaries and bury their eggs and larvae in the substrate (DeVries, 1997, Fausch et al., 2001). Species like pike need floodplain habitat for spawning and nursery areas (Brodeur et al 2004, Casselman & Lewis 1996, Górski et al 2010). To support such activities timing of floods is very important.

Post-disturbance effects

Overall the most important effect of extreeme flooding is change in species composition towards fish species that are better adapted or even dependent on floodplain habitats (Bayley 1991, Jurajda et al., 2006, Maher 1994, Leitman et al 1991). However, true floodplain specialists among fishes depend on long-term isolated floodplain water bodies where they have competitive advantages due to their ability to cope with anoxic conditions (Grift et al 2006, Navodaru et al 2002, Schomaker & Wolter 2011). In contrast, frequently inundated floodplain water bodies are commonly colonized by disturbance-tolerant, eurytopic fish 9Grift et al 2001). The floodplain and tributary habitats accessed during the flooding serve then as nursery habitat for juvenile fish and a source for repopulation of downstream areas.

Similar patterns have been documented for macroinvertebrates (Cortes et al., 2002, Fleituch, 2003, Ward, 1976). Thus, floods promote natural selection of native species and may also increase biodiversity (Lake 2007). It has been also documented that floods play an important role in the elimination of exotic species as native species are better adapted to the regional specificity of these events (Valdez et al 2001).

Due to high mobility of aquatic organisms the recolonization of evacuated areas takes place rapidly. Some studies have observed reduction of diversity and abundance of invertebrates shortly after a flood, followed by very quick recovery (Stubbington et al., 2009). Fish species also are quick to recolonize, although the speed is strongly dependent on availability of refugia (Townsend, 1989). Furthermore species composition and densities also depend on the morphological alteration caused by floods (Elwood and Waters 1969). The available flooded areas will also determine fish productivity, growth and survival and, accordingly, density of juveniles' year classes, especially in spring.

Droughts

Concurrent response

Reduction of habitat area during drought conditions is not only due to a smaller wetted area but also due to loss of habitat suitability. Generally this leads initially to higher concentration of individuals. Many fish change their behavior adjusting to the new conditions. Hierarchical dominance and territoriality disappear and migration in search for suitable refuge habitats takes place (Elliot 2006, Dekar & Magoulick, 2007). For organisms preferring shallow and low velocity zones (e.g. invertebrates and juvenile fish) or that are tolerant to high temperature and low oxygen, the suitable area may initially increase. As wetted area further declines the densities of these organisms increase (Dewson et al., 2003, McIntosh et al., 2002) and as food availability declines and predation increases the numbers of invertebrates decline, and fish assemblage structure changes (Arthington et al., 2005, Wood et al., 2000). However, fish recruitment is may sometimes be the strong following a drought year, demonstrating resilience of these species (Keaton et al., 2005).

As large portions of aquatic zones become terrestrial sedentary and sessile species such as freshwater mussels are at some risk of stranding and predation. The temperature increase in expanding shallow margins expose them also to thermal shock (Castelli et al 2012, Figure 18).

Figure 18 - Mussel in drying up floodplain lakes in the Rhine Delta during drought May 2011 (Photo T. Buijse).

In perennial streams richness of macro invertebrate species declines due to loss of habitat diversity. The same phenomenon leads to local increase in fish species richness in remnant pools (Pires et al., 2010). Again predation by fish and other vertebrates becomes a limiting factor (Labbe & Fausch, 2000). The high densities in the pools and consequent stress may support an outbreak of parasitism (Maceda-Veiga et al., 2009).

Post-disturbance changes

The overall consequence is a change in species composition towards drought tolerant, small bodied species, i.e. those for which habitat conditions have actually improved. As drought persists and water quality reaches lethal levels the numbers of individuals rapidly decline (Extence 1981). For fish the timing of drought is important as it may affect the sensitive life stages such as spawning or egg incubation, shaping community composition during following years, by changing abundance of an entire year class. In natural systems this will be balanced by other years with strong recruitment. Short-term drought is very fast for fish as well as invertebrates. Recovery from longer-term droughts that span multiple years becomes very limited due to the small pool of survivors. The effects of supraseasonal droughts are difficult to predict because of our limited knowledge of the impact of these events (Lake, 2007).

Biological response intensity and direction

The intensity of biological response depends to the greatest extent on their predictability derived from hydrological events periodicity (e.g., Moffett 1936, Hoopes 1974, Poff 1992). Through natural selection, we can assume that populations are developed by adaptations to the conditions that are most frequent. The frequency of occurrence in the past is a function of the predictability of an event. Events that are rare are inevitably those to which organisms are least adapted; hence their impacts are the most severe.

Of course the frequency is also related to the magnitude and duration of disturbance events. This relationship between these measures of event intensity and frequency is generally described by a power law (Bak 1996). The disturbances of large magnitude or duration are much less frequent and vice versa. Consequently, the events of extreme magnitude and/or duration (floods or droughts) can be expected to have a much stronger biological effect, such as they may cause the depletion or expansion of populations. This concept is presented in Figure 19 using a log-log plot.

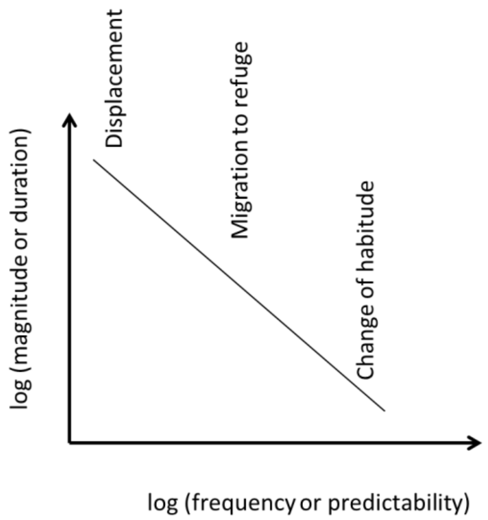


Figure 19 - Hypothetical biological response to disturbance drivers.

However, at this point it is difficult to establish specific thresholds delineating such catastrophic conditions. Indirect attempt is by investigating the historical habitat time series and isolating events that are very rare. The technique called Uniform Continuous Under Threshold analysis investigates the frequency of continuous habitat shortage events caused by low flows and defines the magnitude of the least rare event as a disturbance threshold (Parasiewicz et al 2007). Prolonging of the event duration beyond some threshold may lead to biological response equivalent to the catastrophic. Parasiewicz (2007) defines these as events of decadal frequency. The same logic can be applied to predictable floods, although the overall direction of the response may be the opposite i.e. dramatic increase of diversity abundance and biomass as a consequence of prolonged floods rather than decline. The unpredictable floods (e.g. unseasonal or happening with higher frequency than in the past) have been documented as having very deleterious effects on the fish fauna (e.g., Moffett 1936, Hoopes 1974). We can therefore conclude that the physical measure related to intensity of biological response is historical frequency of occurrence.

This review of the published information allows recognition of a general pattern of the biological response indicating that the occurrence of both types of may lead towards a **change in aquatic community structure**, limiting the organisms less adapted to the disturbance and promoting those with better adaptations (eg. Boix et. al 2010). Another general observation is that predictable floods tend to increase fish species richness, abundance and biomass and droughts lead to a decline (Figure 20). During flooding the mechanisms leading to these changes are on the one hand drift, injury and habitat modification during and after the flood. In lowland floodplain rivers the occurrence of hydraulically unsuitable habitats (very fast) is compensated by the creation of vast areas of very attractive spawning as well as rearing and growing habitats in the floodplain. In high gradient rivers floods open access to tributaries effective expanding accessible habitat area. This causes net gain in populations at the segment and landscape unit scales. At reach and finer spatial scales, the response types are changes in habitude, drift, migration to refuges and feeding grounds, and spawning.

Drought in contrast leads at coarse scales to net loss of population size caused by habitat limitation, predation and food shortages. However, diversity increases. The biological response types at the reach and finer scales are changes in habitude, stranding, migration to refuges, exhaustion.

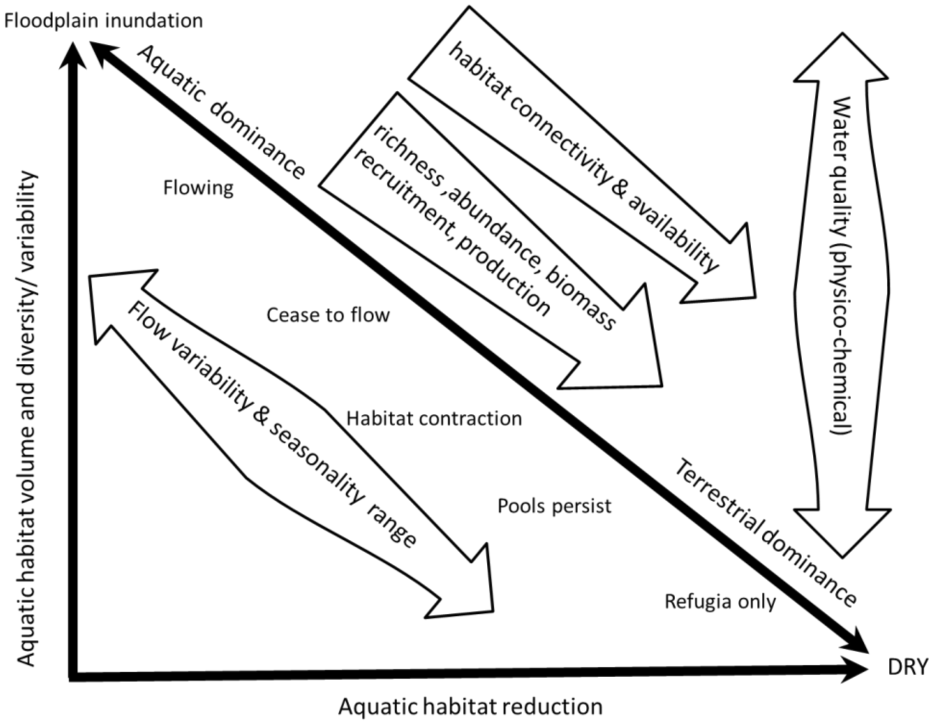


Figure 20 - Conceptual overview of fish responses to changes in flow habitat characteristics (modified from Webb et al. 2010). The model hypothesizes that with reduction of flow, there will be negative effects on the behavioural and reproductive characteristics of native fish and a decrease in population and community composition measures. Conversely, the same changes in flow habitat are hypothesized to increase the dominance, spread and abundance of terrestrial fauna and flora. The figure highlights the generic relationships between reductions in flow habitat and freshwater fish, and stresses that as well as a reduction in discharge leading to overall reductions in habitat, it also leads to reduced diversity in habitat and reduced water quality. All of these proximate agents are expected to impact on native fish assemblages.

Presented model is very generic and some studies suggest different results for individual cases. One of most significant covariates is morphological variability of river and floodplain. It not only dampens down deleterious impacts by providing refugia but also by offers diversity of habitats increasing richness, abundance, biomass, recruitment and productivity.

According to Lake (2000) floods are the pulse disturbance and the response to floods is most often of a pulse type. Extreme floods that cause dramatic HYMO change will cause press response. In both cases flood magnitude is a stronger driver than event duration. Since droughts are presses and ramps the drought response is a ramp. Here, the key driver is the duration (Figure 21). Increased frequency of disturbance events is also a driver of ramp response. For example increased frequency of drought events that happen during supra-seasonal droughts will weaken the physical condition of fauna, may deplete the populations, and lead to catastrophic consequences.

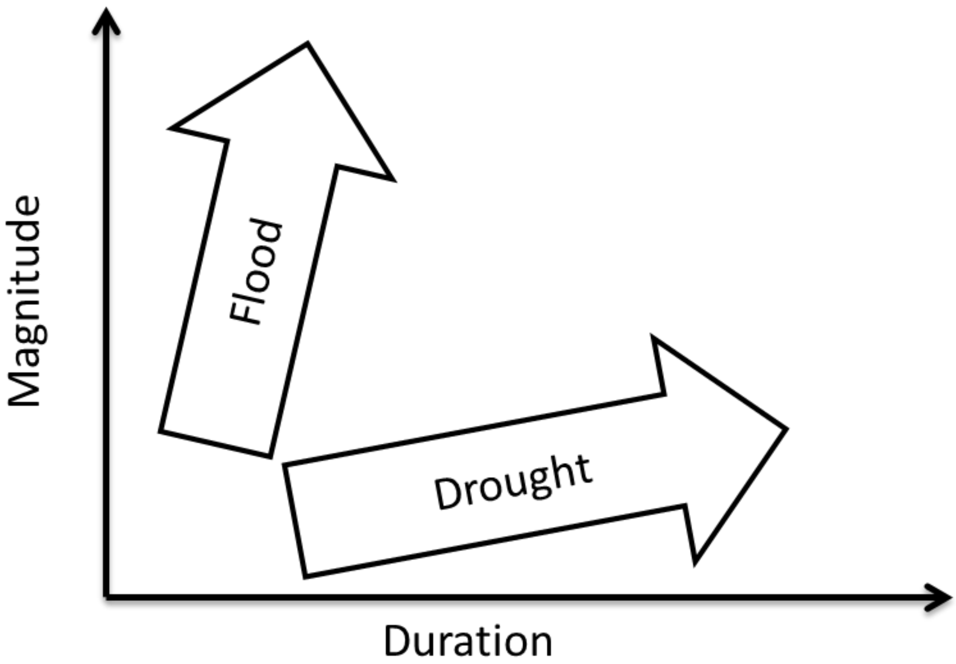


Figure 21 - Factors driving intensity of biological response to floods and droughts

Examples for Floods and Droughts

Dependence of biological response

The intensity of biological response also depends upon factors such as geographic location or seasonality. A drought of the same magnitude will have different consequences in northern and southern Europe. In some Mediterranean streams fish can survive complete dryness that would be lethal to any northern organisms. Since the reason is adaptation of organisms to regional conditions the metric here is predictability i.e. historic frequency of events. This geographic specificity is responsible for better survival of native vs. introduced species (Meffe 1984).

Similar mechanisms are associated with disturbance timing. Severe flooding in midsummer will have different biological consequences than during the spring (spawning) time. Since summer flows are mostly characterized by low flow conditions, the majority of animals utilize habitat for rearing and growth, with extensive nursery habitat. Flood disturbance is not expected and may have a catastrophic impact on juvenile fish. In spring time the flows are usually high due to precipitation and snowmelt and many fish are utilizing them for spawning.

One boundary factor influencing the resistance and resilience of species that is not necessarily related to event predictability, is availability of refuge and habitat patchiness (Lake 2000). Many studies documented that refugia have a direct effect on survival of animals and are decisive for the speed and range of recolonization (Covich et al., 2003, Fenoglio et al., 2006; Lancaster & Belyea, 1997; Lake, 2007). They protect the fauna from high velocities as well as from the effects of water quality limitations. The availability of refugia is strongly related to the river type and its morphological diversity. As reported by Hickey and Salas (1995) the biological consequences of flooding are very different in high-gradient, rivers lacking floodplains, than in large low-gradient floodplainrivers. In the former, the impact direction is negative, leading to losses in the fish and invertebrate fauna. In low gradient rivers, an increase in population density and productivity can be expected, because the floodplain not only offers refugia but also attractive feeding grounds. Therefore, we can assume that the river planform is a stronger factor than geographical location.

Table 5 - Biota shaping factors at different scales

Flood HYMO factors	Biological response	Indicative space scale	Scale linkages	Indicative event frequency	Drought HYMO factors	Biological response		
Spatially variable mosaic of events	Metapopulation shaping, maintenance and diversification	>10^4 km^2	**Region**	**>10^3years**	Spatially uniform events blanket	Metapopulation shaping, maintenance and unification		Resilience
Maintenance of dynamic equilibrium	Population maintenance	10^2-10^4 km^2	**Catchment**	**10^2-10^3 years**	Maintenance of dynamic equilibrium	Population maintenance		
Channel form variation	Change in biodiversity, sub-population reset, species extinctions and recruitment	10^2-10^3 km^2	**Landscape unit**	**10^2-10^3 years**	Severed links between streams and catchment	Change in biodiversity, sub-population reset, species extinctions		
Channel reconfiguration	`Change in community structure	10^1-10^2 km^2	**Segment**	**10^2-10^3 years**	Connectivity loss, reduction habitat area and nutrient fluxes	Change in community structure, refuge migration		
Patch redistribution, habitat expansion	Out of habitat refuge and exploration, displacement, injuries	10^{-1}-10^1 km^2 (20+*widths)*	**Reach**	**10^1-10^2 years**	Patch redistribution, habitat shrinking, more shallow margins	Out of habitat refuge (pools, springs) , increased survival of fry and juvenile fish	Resistance	
HMU type change	within-habitat refuge	10^0-10^2 m^2 (1-20 widths)	**Geomorphic Unit**	**10^0-10^1 years**	HMU type change, more shallow margins	within-habitat refuge, stranding		
velocity, depth, substrate	Habitude adjustment, outmigration	10^{-1}-10^1 m^2 (5-20 D_{50})	**Hydraulic Unit**	**10^0-10^1 years**	velocity, depth, substrate	Habitude adjustment, outmigration, increased predation		
		10^{-2}-10^{-1} m^2 (10^0-10^1 D_{50})	**River element**	**10^0-10^1 years**				

Region

At the regional scale disturbances shape the composition of metapopulations and overall biodiversity. This occurs through a patchwork of disturbances of various intensity, differently affecting different catchments. All are driven by significant meteorological and landscape variation. Since floods have a smaller spatial reach than droughts and their effects are more dependent on the topography (steeper catchments will react differently to low gradients unconstrained areas) or surficial geology, their effects are more diverse in the region than the effects of droughts. Droughts have a more regional character and affect populations more uniformly. Hence predictable floods increase the populations size and droughts reduce it and both may balance each other. Still, depending on the stream productivity, both disturbance types may increase biodiversity (e.g. Ilg et al 2009, Lake 2000). The driving biological process is at this scale resilience.

Catchment

At the catchment scale disturbance shapes community composition within the population. The assemblage of predictable floods and drought events, which have opposite response directions, together with rare unpredictable events, may maintain dynamic equilibrium of the catchment. This shapes aquatic communities and subsequently maintains population structure and viability. The driving biological process is at this scale resilience.

Landscape Unit

Floods are responsible for maintenance of channel form variation through e.g. removal of sediment deposits and maintenance of braided, meandering or straightened channel types. They improve connectivity and allow for species exchange and recruitment. This in turn defines the community composition, population age structure and biodiversity of sub-populations. Droughts in turn limit the connectivity between the communities, severing the links between streams and catchments. This can be through closing in-channel migration pathways or floodplain sedimentation. The consequence is decline in abundance and modification of community composition and age structure, resetting subpopulations to pioneer organisms. The driving biological process is at this scale resilience.

Segment

At the segment scale, floods reconfigure the channel by modification and redistribution of hydromorphological patches. This creates a new habitat mosaic that reshapes the community. Some organisms boom while others loose their habitat. The change in community structure (age, sizes, abundance), through availability of productive habitats during the flood events, further modifies species composition. Droughts limit habitat area, its connectivity and nutrient input. This triggers emigration to refuge areas, loss of abundance, biomass and in consequence altered species composition in the community. The driving biological process is at this scale resilience.

Reach

HYMO of reaches is modified by floods through the redistribution of Geomorphologic Units during and after the flood. During the flood the habitat expands and HYMO diversity changes into pattern of fast flowing channels and refuges in inundated areas. Overall the distribution of hydromorphologic units (HMU), which are features created by geomorphic units and hydraulic conditions (Parasiewicz 2001), becomes more uniform. The HMUs increase in size and are dominated by runs (Figure 22). This provokes migration to out-of-habitat refuges (Lake 2000). Post flood, the distribution of HMUs and subsequently habitats changes, creating a new biophysical template for distribution of individuals. Consequently the faunal composition of the reach also changes.

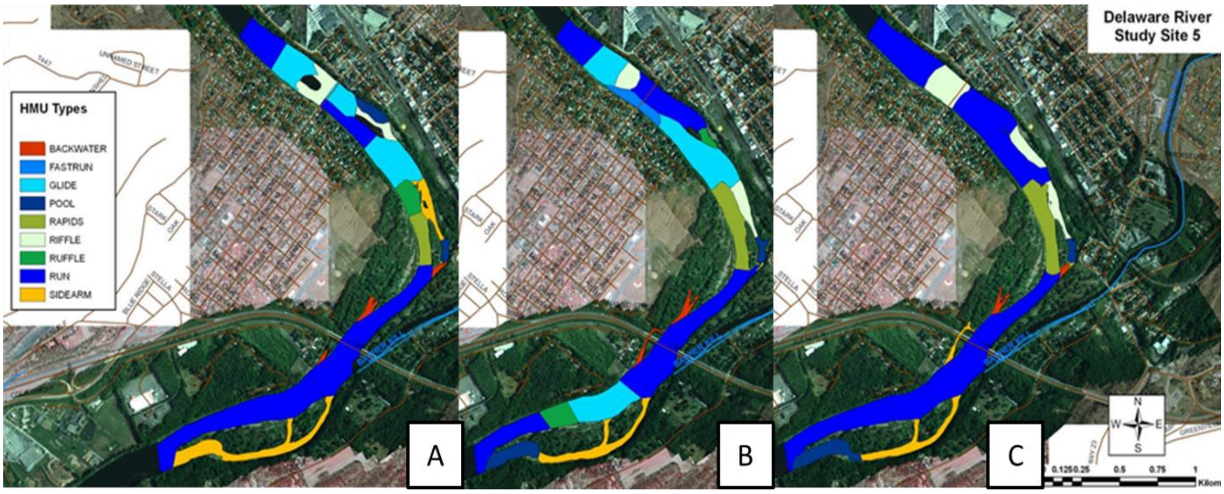


Figure 22 - Changes in habitat distribution at 3 increasing flows mapped on the Delaware River, NJ. A) flow of 5 $ls^{-1}km^2$, B) 11 $ls^{-1}km^2$, c) 16 $ls^{-1}km^2$

Droughts have similar mechanisms but contrasting effects. The HMU mosaic changes towards smaller and shallower units. The bed topography and roughness have a strong influence on the distribution of flow velocities and depth, hence habitat types. This provokes emigration into out of habitat refuges. After the drought the HYMO conditions typically do not change unless the drought ends with severe storms, which can erode the channel. As visible at this scale the resistance is as important of biological action as resilience .

Geomorphic Unit (GU)

At the scale of the GU the floods and droughts cause change of hydraulic conditions in the units expanding or shrinking their influence. The events can also change the GU geometry through erosion and sedimentation. At this scale the response is to search for refugia within-habitats (Lancaster and Belyea 1997), which at least for invertebrates is the most common type of refugium. Hence at GU scale the response is resistance and redistribution of the organisms within and modification of species composition post disturbance.

Hydraulic Unit

The hydraulic units are fields of uniform depth, velocity and substrate within the GU. Disturbances are having very similar effects to those at the GU level. The hydraulic units, may change hydraulic character (e.g. from slow to fast), expand or shrink. The biological response is resistance and therefore first habitude adjustment and outmigration to the more adequate units.

River Element

At the scale of river elements the processes are the same as in hydraulic units, but affect smaller organisms such as macroinvertebrates and small fish. The driving biological process is at this scale resistance.

5.2 Ecological responses to floods and droughts in Europe

5.2.1 Introduction

The goal of this sub-chapter is to provide a Europe-wide evidence-based catalogue of ecological responses to quantified hydrological extreme events: naturally occurring floods and droughts. In contrast to section 5.1, which takes the form of a narrative review that is based on a worldwide set of publications, in this section (5.2) we present a systematic review and a first attempt at a meta-analysis, limited geographically to the European continent. The main product of this work is the Ecological Responses to Floods and Droughts Catalogue (hereafter referred to as the "ERFD Catalogue") that has the form of a relational geodatabase storing different cases of unique "hydrological event – ecological response" associations extracted from publications identified within a literature search. Wherever possible, hydrological events are quantified using data from the "Objective drought and high flow catalogues for Europe" (Parry et al. 2011) created within the Water and Global Change (WATCH) project. The ERFD Catalogue contents allows for both qualitative and quantitative analyses that increase knowledge of the role of floods and droughts of different magnitude/frequency on the response of aquatic and riparian organisms. An example of such analyses is presented in the Results section in this sub-chapter. In particular, these analyses enable investigation of the relationship between the severity of the extreme events and the direction/magnitude of respective ecological responses.

Lake (2000) stated that the progress in better understanding of the disturbance-response relationships in aquatic ecosystems can be achieved by using quantifiable measures of both the disturbances and the subsequent responses by the biota. However, to date little has been done with this respect. Our study is probably the first attempt to link data on hydrological extreme events in Europe with the responses to these extremes extracted from peer-reviewed ecological literature. Edwards et al. (2012) concluded in their review report on the effects of droughts and summer floods that the European body of literature in this topic is small in comparison to Australia and America. Our systematic review also confirmed this fact. Furthermore, Lake (2011) complained in his state-of-the-art book on the effects of drought on aquatic ecosystems that "hydrological drought indicators are very rarely used to characterize the drought under investigation" (in ecological literature) and that as a consequence, "it is difficult to make firm comparisons between droughts in different localities, or even between different droughts occurring at different times at the same locality". In our opinion, this remark is also applicable to floods. Using the drought and high flow catalogue to link extreme events with biotic responses in our study we provide an original attempt to address the problem formulated by Lake (2011). To our knowledge, the only study that has used a similar approach of systematic review and quantification of ecological responses is that of McManamay et al. (2013). However, their database contained examples limited to the South Atlantic region of the United States, and more importantly, it dealt with various types of both natural and anthropogenic flow alterations, among which floods and droughts were only two examples.

We follow the terminology introduced by Lake (2011), i.e. whenever we refer to "disturbances", "responses" and "perturbations", we mean, respectively, the following:

- "disturbances" – hydrological extreme events, i.e. either floods or droughts, understood here as (natural) events, i.e. having a particular time of occurrence defined by the beginning and ending date;
- "responses" (to the disturbance) – impacts of a certain event on biotic/abiotic components of the ecosystem;
- "perturbations" – disturbances and responses considered together.

Since the focus of this section is on biota, when referring to responses we will mainly mean the biotic, not abiotic, responses. At this stage we used the assessment of the authors of a case study on the impact of the studied extreme event on the biota (positive, negative or neutral). In general, positive responses corresponded to increases in various ecological metrics, whereas negative responses to decreases of these metrics. Neutral responses usually corresponded to insignificant changes (Table 6).

Table 6 – Examples of terms describing ecological responses in the studied papers categorised into broad response classes.

Assigned response categories	Example response descriptions extracted from the papers
Positive	Increasing in assemblages variability
	Increase in the abundance
	Rapid increase in numbers of idividuals, faster development and growth
	Increase in diversity and density in numbers
Neutral	No significant changes
	No evidence of loss of species richness
	Used pools as the refugia
	Had little effect on abundance
	High resistance to the changes
Negative	Mass mortality
	Reduction of the species number
	Decrease in abundance
	Reduction in the total number of individuals and the dominant taxa

5.2.2 Methodology

Literature reviews are used to combine knowledge from multiple studies in a given topic, and to summarise the latest evidence. They can have either a narrative or a systematic form. Systematic reviews aim to reduce bias present in narrative reviews by using explicit methods to perform a comprehensive literature search and critical appraisal of the individual studies. Systematic reviews sometimes use a statistical framework, meta-analysis, to combine the data from the literature search to produce a single estimate of effect (Crowther et al. 2010, Harrison 2011).

Systematic reviews and meta-analyses are most widely used in medicine (e.g. Crowther et al. 2010). However, they are also applied in ecology (Harrison 2011). Notable examples include: a study estimating how current climatic conditions, climate change and habitat loss interact and impact on terrestrial ecosystems (Mantyka-Pringle et al. 2012); a study quantifying effects of aquaculture on living and non-living suspended fractions of the water column (Sara 2007); a study assessing how riparian vegetation responds to increased summer drought (Garssen 2014); and the aforementioned study on the ecological responses to natural and anthropogenic changes in streamflow across the South Atlantic Region of the USA (McManamay et al. 2013).

In this study we have adapted the methods of systematic review and meta-analysis to the problem specified in the Introduction for several reasons:

- There is no common methodology for investigating the ecological effects of floods and droughts that is approved and used by the majority of researchers. This is partly explained by the stochastic nature of these events, which makes it difficult to plan field surveys in advance. In the case of droughts in Europe, most of the studies deal with low flows, and not droughts *per se* or deal with intermittent streams that are better adapted to droughts than permanent ones and none of the studies they investigated followed the rigorous BACI design (Before-After Control-Impact; cf. Smith 2013) (Edwards et al. 2012).
- Ecological response is a very broad term encompassing two major properties: resistance (capacity of the biota to withstand the stresses of a disturbance) and resilience (capacity to recover from the disturbance) (Lake 2000). In practice different studies analyse different aspects of ecological response for different biota, e.g. for fish: changes in abundance, biomass, density, recruitment, migration, etc.
- There is a large diversity among investigated studies that makes any comparison or integration of findings challenging. This diversity arises from the whole spectrum of spatial (from small streams to large rivers) and temporal (from flash floods lasting a few hours to supra-seasonal droughts) scales, from the biogeographical and hydromorphological variability of sampling sites, and finally from different hierarchical levels of assessment: on communities, families, or individual species.

Figure 23 illustrates the logical framework of the applied methodology. In the first step a search strategy is designed and literature search is performed. This can result in a wide range of publications that has to be narrowed in the next step through using various inclusion and exclusion criteria. In parallel to these steps, a relative geodatabase storing data and information extracted from the identified set of publications is designed and implemented in selected software. As soon as the database schema is ready, the (technical) extraction protocol is designed, database operators (data extractors) are trained, and the insertion of records starts. In parallel to this step, for each hydrological extreme event recorded in the database, the values of hydrological indices quantifying this event are calculated and inserted into the database based on the “Objective drought and high flow catalogues for Europe” (Parry et al. 2011), hereafter referred to as the “WATCH Catalogue”. This step is marked in a red box in Figure 23. because it can be performed only for a subset of all records from the ERFD Catalogue; those which overlap geographically with data available in the WATCH Catalogue. After completing this step, the geodatabase as the final product is ready, and the analytical part can start. This can involve basic statistical summaries, qualitative and quantitative analyses linking explanatory variables with outcome variables, and more sophisticated statistical meta-analyses. This leads to an evidence-based research synthesis and enables drawing conclusions.

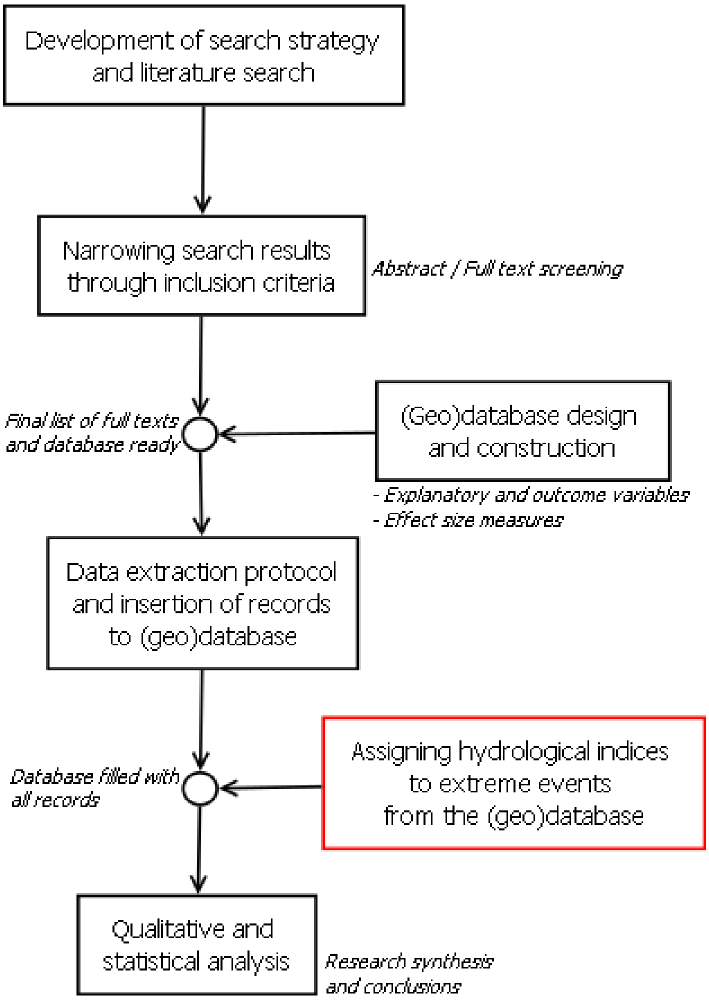


Figure 23 - The logical framework for meta-analysis of ecological responses to floods and droughts in Europe.

Literature search of scientific peer-reviewed studies (journal and conference proceedings articles) was performed using the Thomson Reuters Web of Science Core Collection. An optimal set of keyword strings was selected on a trial and error basis (Table 7). The final set consisted of three expressions joined by an "AND" operator: one related to hydrological extreme events, one related to biota types and the last one related to the ecosystem name. The search was restricted to research categories connected to freshwater ecology. The number of records was 7532. Therefore in the next step the keyword string was extended by another expression including all the names of European countries and major regions and excluding all the names of continents and major countries outside Europe to focus the number of records. The new search resulted in 1762 records which were all analysed in the next step of consecutive narrowing of search results. This indicates that only approximately 23% of the worldwide peer-reviewed literature in this topic deals with case studies in Europe, which is in agreement with the previously mentioned remarks from Edwards et al. (2012).

Table 7 - Characteristics of the Web of Science literature search.

Feature	Description
Topic	(drought OR flood OR "high flow*" OR "high discharge*" OR "low flow*" OR "low discharge*" OR spate*) AND (fish* OR spawn* OR *invertebrate* OR vegetat* OR plant*) AND (river* OR stream* OR floodplain)
Category	Environmental Sciences OR Ecology OR Marine Freshwater Biology OR Water Resources OR Geosciences Multidisciplinary OR Fisheries OR Geography Physical OR Plant Sciences OR Biodiversity Conservation OR Zoology
Document type	Articles OR Conference Proceedings
WOS Citation Indexes	SCI-EXPANDED & CPCI-S
Number of records	7532

Firstly all records with irrelevant titles were excluded from the list. The second step of narrowing the search results was based on the specific inclusion and exclusion criteria shown in Table 8. In most cases, abstract reading enabled an assessment of whether a given publication was suitable or not. In other cases, full text screening had to be performed.

In parallel to the Web of Science search, an effort was made to increase the number of publications by including those which fulfill all selection criteria but are not present in the Web of Science Core Collection. Email enquiries were sent to a number of scientists involved in the REFORM project as well as to other well-known experts in the field. The response rate was moderate, and many of the suggested papers did not fulfill at least one of the selection criteria and so they were excluded. One journal not indexed by the Web of Science (Limnetica, in Spanish) was identified and searched, which resulted in five new publications. Two more articles were identified upon examining publications citing the set of already identified publications using Google Scholar. The total number of suitable papers finally identified was 70.

Table 8 - Publication inclusion and exclusion criteria.

Category	Inclusion criteria	Exclusion criteria
Research character	Field studies	Non-field studies (e.g. mesocosm, laboratory or statistical)

Category	Inclusion criteria	Exclusion criteria
Disturbance type	Natural flood & drought events	Hydropeaking, experimental floods etc.
Time period	Event dates (at least approximately) specified and within period 1961-2005 (WATCH Catalogue)	No dates specified or outside the period of interest
Ecosystem type	Lotic ecosystems (regardless of scale)	Lentic ecosystems
Ecological focus	Fishes or macroinvertebrates or (aquatic/riparian) vegetation	Other biota (e.g. algae, bacteria, etc.)
Study location	Well defined and inside Europe	Not defined or outside Europe
Event-response	Ecological responses can be attributed to single events	Statistical approaches not permitting to link responses to single events

In parallel to the publication search, a geodatabase was designed in which various information and data extracted from publications could be stored and managed in an organised and efficient manner. To this end, ESRI ArcGIS 10.1 software and its native file geodatabase format was selected. This data model is suitable for storing and managing both geospatial and non-spatial table data and is based on relational principles (Childs 2009). Furthermore, its data structure is optimised for performance and storage, and editing is user-friendly.

The ERFD database was designed in ArcCatalog. Its core part consists of three objects:

1. Table "Publications" storing references to all publications identified in literature search.
2. Point feature class "Sites" (stored in a feature dataset "Sites") storing geographical location of sites in which sampling was carried out as well as several basic geographical attributes of these sites.
3. Table "Perturbations_relationship" storing various descriptive and quantitative information on all individual cases of perturbations identified from selected publications.

Objects 1 and 3 as well as 2 and 3 are connected to each other through two so-called relationship classes. Relationship classes in the geodatabase manage the associations between objects in one class (feature class or table) and objects in another class. In our case, one publication can contain many examples of perturbations (e.g. on different biota types, in different time periods or in different sites). A 1-N ("One-to-many") relationship class represents this relation. On the other hand, one site can be associated with many examples of perturbations (e.g. on different biota types, in different time periods or coming from different publications). This relation is also represented by a 1-N relationship class. Hence, the "Perturbations_relationship" table is an intermediate table that links the "Publications" table with a "Sites" feature class through a relationship class of an effective cardinality N-M ("Many-to-many"). In other words, in each site perturbations from multiple publications can occur, and at the same time in each publication perturbations occurring in multiple sites can be present. Further explanation of this relationship as well as of the attributes of respective tables and feature classes is provided in Figure 24.

Table 9-Table 11 present descriptions of all fields from the table attributes of the main geodatabase objects. Most of the fields can be used to stratify analysed cases by various categories, e.g. event type, biota type, basin area category, etc. The main outcome field is the "Response direction" which evaluates the direction of ecological response as one of three values: negative, positive or neutral. In this assessment we relied heavily on author interpretation as in McManamay et al. (2013).

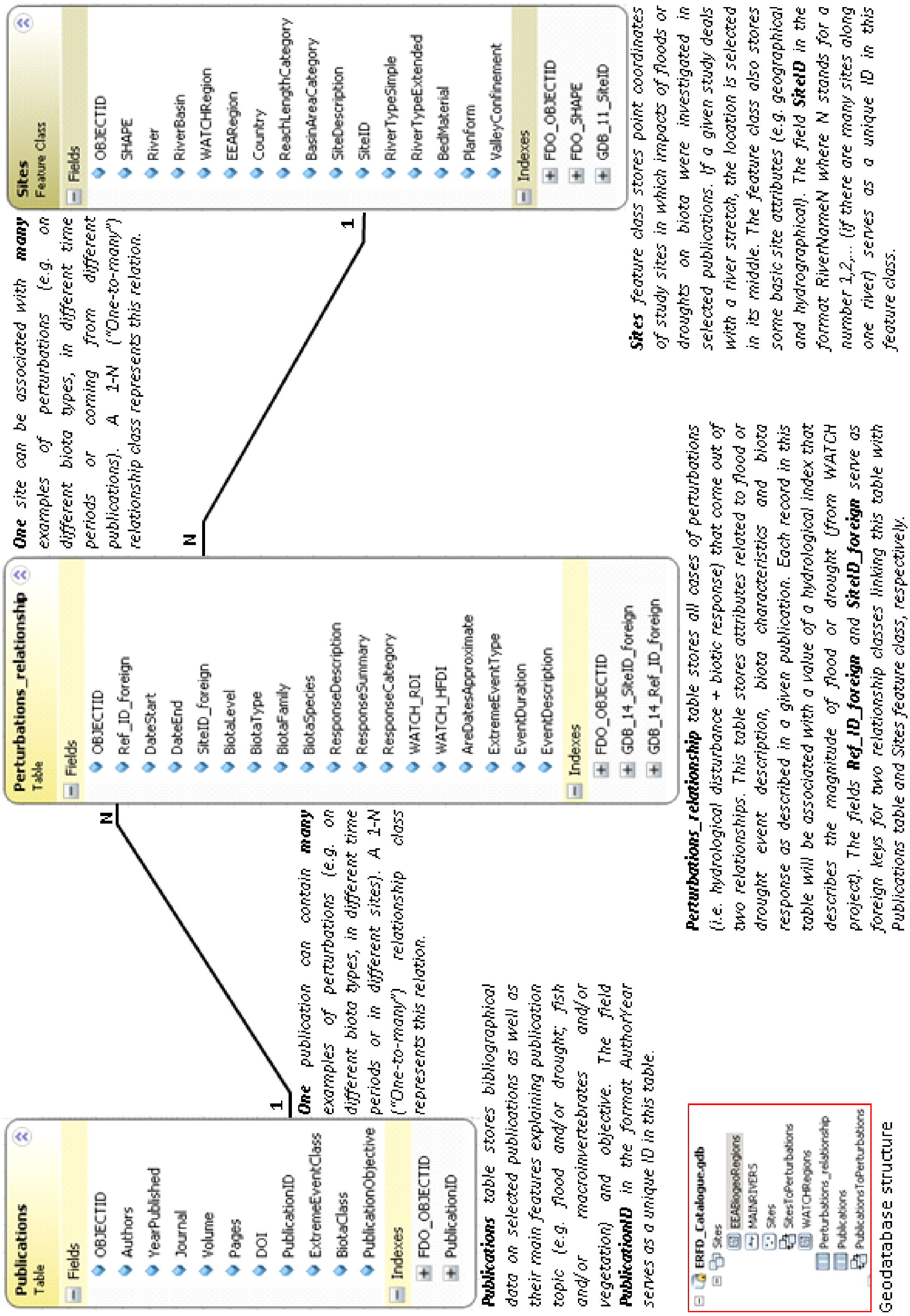


Figure 24 - Relational geodatabase schema as implemented in ArcGIS 10.1.

Table 9 - Field descriptions from the "Publications" table.

Field name	Data type	Field description
PublicationID	Text	A unique ID of a publication in the form AuthorYear
Authors	Text	Author names
YearPublished	Integer	Publication year
Title	Text	Publication title
Journal	Integer*	Journal name
Volume	Text	Volume number
Pages	Text	Page numbers
DOI	Text	Digital object identifier
ExtremeEventClass	Integer*	Type of hydrological extreme event discussed in a given publication: flood, drought or flood and drought
BiotaClass	Integer*	Type of biota discussed in a given publication: all 7 possible combinations of fish, macroinvertebrates and vegetation,
PublicationObjective	Text	Publication objective description extracted from the paper introduction

* coded value domain

Table 10 - Field descriptions from the "Sites" feature class attribute table

Field name	Data type	Field description
SiteID	Text	A unique ID of a sampling site coded by the name of the corresponding river and optionally a number (in case of many different sites along the same river)
River	Integer*	Name of the river on which study site is located
RiverBasin	Integer*	Name of the river basin to which the study site belongs
WATCHRegion	Integer*	Name of the WATCH region (Parry et al. 2011) to which the study site belongs
EEARegion	Integer*	Name of the European Environment Agency biogeographical region by to which the study site belongs
Country	Integer*	Name of the European country to which the study site belongs
ReachLenghtCategory	Integer*	Length of the study transect in kilometers
BasinAreaCategory	Integer*	Approximate catchment area in km^2 upstream from the study site
SiteDescription	Text	Short descripton of the study site extracted from the publication

* coded value domain

Table 11 - Field descriptions from the "Perturbations_relationship" table.

Field name	Data type	Field description
PublicationID_foreign	Text	A foreign key of the relationship with the "Publications" table
SiteID_foreign	Text	A foreign key of the relationship with the "Sites" feature class
EventDateStart	Date	Approximate date when the hydrological event started
EventDateEnd	Date	Approximate date when the hydrological event ended
EventDuration	Integer	Event duration in days
AreDatesApproximate	Integer*	Information about accuracy of event dates determination
ExtremeEventType	Integer*	Information if it's a flood or drought event
EventDescription	Text	Short event description extracted from the paper
BiotaType	Integer*	Type of analysed biota: fish, macroinvertebrates or vegetation

Field name	Data type	Field description
BiotaLevel	Integer*	Hierarchical level of analysed biota: species, family, community
BiotaFamily	Integer*	Name of the family of analysed biota (only if BiotaLevel = "Family")
BiotaSpecies	Integer*	Name of the species of analysed biota (only if BiotaLevel = "Species")
ResponseDescription	Text	Description of the biota response to the given event extracted from the publication
ResponseSummary	Text	Shortened and generalised response description
ResponseCategory	Integer*	Response direction categorised as negative, neutral or positive
WATCH_RDI	Double	Regional Deficiency Index (RDI) calculated only for drought events based on event dates
WATCH_RHFI	Double	Regional High Flow Index (RHFI) calculated only for flood events based on event dates

* coded value domain

In addition to three main geodatabase objects, another three feature classes were stored in the "Sites" feature dataset. These were:

1. Line feature class "MainRivers" storing the main river network of Europe from the CCM2 River and Catchment Database (Vogt et al. 2007);
2. Polygon feature class "WATCHRegions" storing the boundaries of 23 hydrographical regions delineated in the framework of the WATCH Project (Parry et al. 2011);
3. Polygon feature class "EEABioRegions" storing the boundaries of 12 biogeographical regions delineated by the European Environment Agency (http://www.eea.europa.eu/data-and-maps/data/biogeographical-regions-europe).

The main rivers layer was used when adding new records into the "Sites" feature class. Points were snapped to the river network, wherever it was possible.

The WATCH regions were defined based on homogeneous low flow response through a cluster analysis of the DI (deficiency index) time series for each catchment (Parry et al. 2011). The assumption is that catchments in each region respond similarly in their expression of drought. For the sake of consistency, Parry et al. (2011) applied the same regions for high flows. While the detailed methodology of calculating the RDI and RHFI can be found in Parry et al. (2011), a brief summary can be found below.

If the river flow is below (above) the daily-varying Q90 (Q10) threshold, DI (EI) takes a value of 1, signifying that the flow on that day is amongst the lowest (highest) 10% in the period of record relative to normal conditions for the location and time of year. If for a given day and location DI (EI) is equal to 1, this is interpreted that this location is at this time under drought (high flow). Since the daily RDI (RHFI) time series averages a number of binary time series, its values lie between 0 and 1. Thus the daily RDI (RHFI) time series for each region represents the proportion of the region that is under drought (high flow) conditions on that day. RDI (RHFI) values of 0 indicate none of the catchments in a region are being affected by drought (high flows), whereas values of 1 signify the entire region is under drought (high flow) conditions.

Using the "WATCHRegions" feature class allowed points from the "Sites" feature class to be easily associated with WATCH regions. This was, however, possible only for a subset of all sites, as the WATCH regions do not cover the whole of Europe but only those parts for which sufficient amount of discharge data was available (cf. Figure 25).

The layer of the EEA biogeographical regions was used to easily associate each site with a certain EEA region. In contrast to WATCH regions, EEA regions covered the whole Europe, so the association was possible for all sites.

In the next step data from all identified publications were extracted and inserted into the ERFD Catalogue. Since the process of inserting new records was performed by more than one person, a simple protocol of step-by-step rules was created in order to ensure internal coherence. In order to facilitate editing and ensure the attribute table correctness, several geodatabase domains were defined and assigned to certain fields. Attribute domains in file geodatabases are rules that describe the legal values of a field type. For example, coded value domains were assigned to such fields as "BiotaSpecies", "CatchmentAreaCategory" and "JournalNames".

The protocol consisted of the following steps:

1. Adding new codes and descriptions into specific geodatabase domains, whenever necessary.

Inserting new records into the "Publications" table (cf.

2. Table 9 for the field descriptions).
3. Inserting new records into the "Sites" feature class (site location and description based on information provided in a newly added publication, cf. Table 10 for the field descriptions).
4. Adding new relationships between the newly added publication and the newly added site into the "Perturbation_relationship" table (hydrological event characterization, ecological response characterization, cf. Table 11 for the field descriptions).

The following issues were encountered during the data extraction and insertion process, usually due to lack of sufficient information in the analysed papers:

- identification of study site locations (i.e. lack of detailed study area map or coordinates);

- identification of the event dates (i.e. only event year or month mentioned in the text, or no mentioning in the text but only showing hydrographs in figures that were occasionally difficult to read);

- poor hydrological event descriptions (i.e. not mentioning how severe was a studied flood or drought);

- very complex biota responses to disturbance (i.e. hard to classify and occasionally no author interpretation whether the response is positive or negative).

The second above mentioned issue was the most important one, because event dates directly influence the values of the WATCH RDI and RHFI indices. In several cases, the event dates were specified through analysing the time series of the WATCH indices for a given region.

5.2.3 Results

The analysis of 70 publications identified within the search process (inserted into the *Publications* table) has resulted in 96 event-response cases (i.e. "perturbations" added to the *Perturbations_relationship* table) occurring in 79 different locations (added to the *Sites* feature class). Annex D shows the list of investigated papers with a brief summary of analysed hydrological events and broad description of ecological responses on the different taxonomic levels.

The majority of analysed publications were published after 2000 (reaching an annual total of 10 in 2004). Only 4 publications were published before 1990, two in the 1970s and two in the 1980s. The articles were published in 34 different journals with a maximum number of 12 publications in *Hydrobiologia*. Ecological journals were far more frequent than hydrological ones.

Investigated sites were spread across Europe from North to South, although some regions or countries were more represented than others (Figure 25). Approximately 90% of all locations belonged to one of three EEA biogeographical regions: Continental, Atlantic or Mediterranean (26, 23 and 21 sites, respectively). The remaining 10% of locations belonged to Alpine, Pannonian and Boreal regions (5, 2 and 2 sites, respectively). Only about half of the sites were within the boundaries of the WATCH regions, therefore for each point lying outside the WATCH regions we have calculated Euclidean distance to the closest lying region boundary and associated this region with a given point. In 19 out of 41 cases the distance from a given point to the closest region was less than 100 km and we have also included these points in further analyses. The 100 km threshold is arbitrary, but is relatively small compared to the average WATCH region geometrical attributes determined in ArcGIS (i.e. minimum bounding polygon length equal to 511 km).

Investigated sites belonged to 12 countries with UK, Spain, Portugal, Czech Republic, Germany and France being the most represented ones. Over 30 river basins contained the analysed points with The Thames, the Rhone and the Oder river basins occurring the most frequently. For each location an approximate upstream catchment area was calculated and classified according to the order of magnitude. The variability in this respect was huge: all classes from 1-10 km^2 to 100,000-1,000,000 km^2 were represented. Medium-sized rivers (100-1,000 km^2) were the most frequent class.

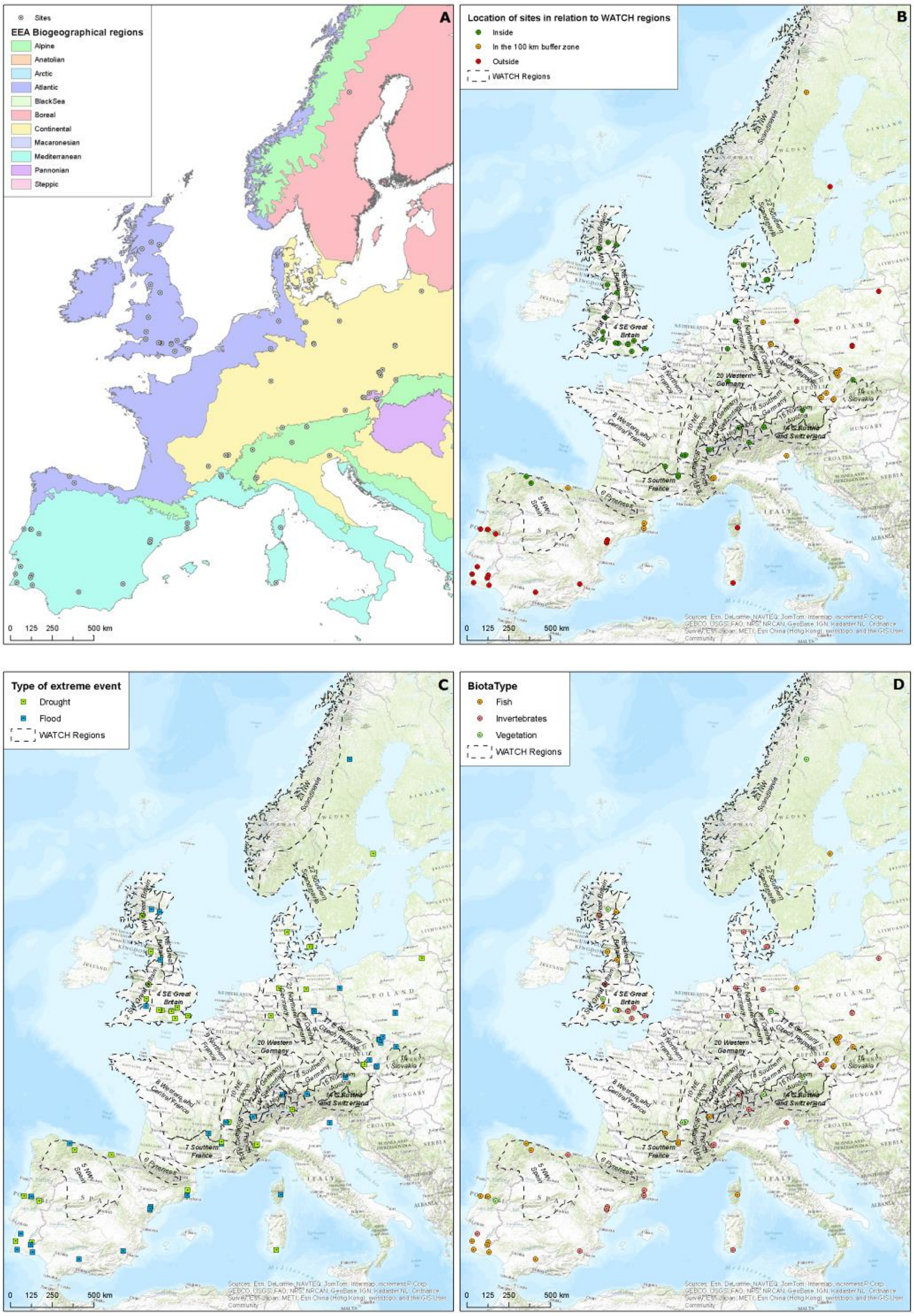


Figure 25 – Maps of identified sites in relation to : A. EEA biogeographical regions; B. WATCH regions; C. types of extreme events; D. biota types.

Out of 96 individual cases, 51 dealt with floods and 45 with drought events. With respect to biota type, 49 dealt with macroinvertebrates, 36 with fish and 11 with vegetation. However, there is a clear relationship between the extreme event types and investigated biota: flood studies are more frequent for fish, while drought studies are more frequent for invertebrates (Figure 26). In over 70% of all cases the ecological response was investigated at the community level. Relatively few cases dealt with single families or species, although in the case of fish, single species studies were far more frequent than in the case of macroinvertebrates (Figure 27).

Mean duration of flood and drought events was equal to 19 and 167 days, respectively. The 1976 and 2003 droughts were the most frequently reported (in 9 and 6 cases, respectively). Floods that occurred in 1997 and 2002 were the most frequently studied (both in 9 cases). The statistical distribution of both indices was quite similar (Figure 28). The mean value of RDI was slightly higher than the mean of RHFI (0.36 and 0.3 respectively). Higher index values reflect either a more rare extreme event or an event taking place more uniformly across a given region. It should be noted that the flood events especially in small catchments are more likely to be missed or misrepresented in the WATCH index time series than the drought events due to local rather than regional nature of this kind of hydrological extreme events.

Characterization of ecological responses was qualitative only and in most cases relying on author interpretation. The most frequent type of responses across all studies was "negative", in particular for the studies on droughts (Figure 29). In the case of floods positive and neutral responses were quite frequent as well. Negative responses were predominant in the studies on macroinvertebrates, while for the studies on fish, negative and neutral responses were occurring with similar frequency. In the case of vegetation, neutral responses were the most frequent.

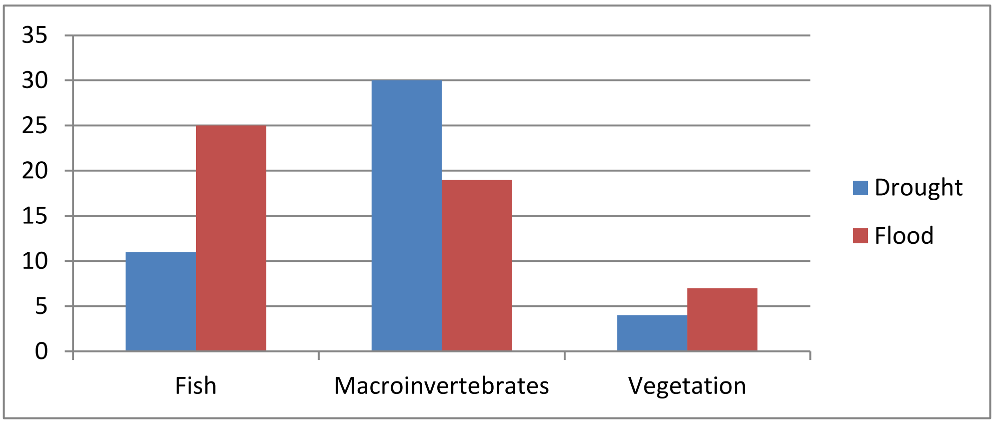


Figure 26 – Number of cases dealing with different biota types and different extreme event types.

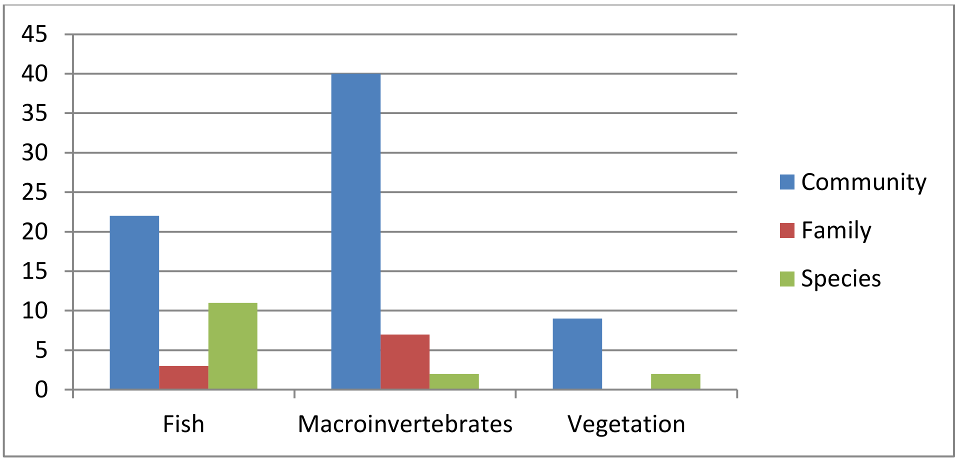


Figure 27 - Number of cases dealing with different ecological levels.

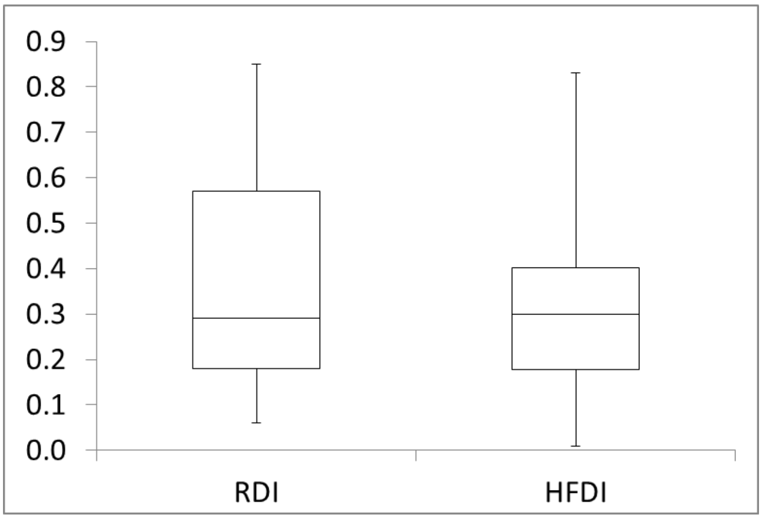
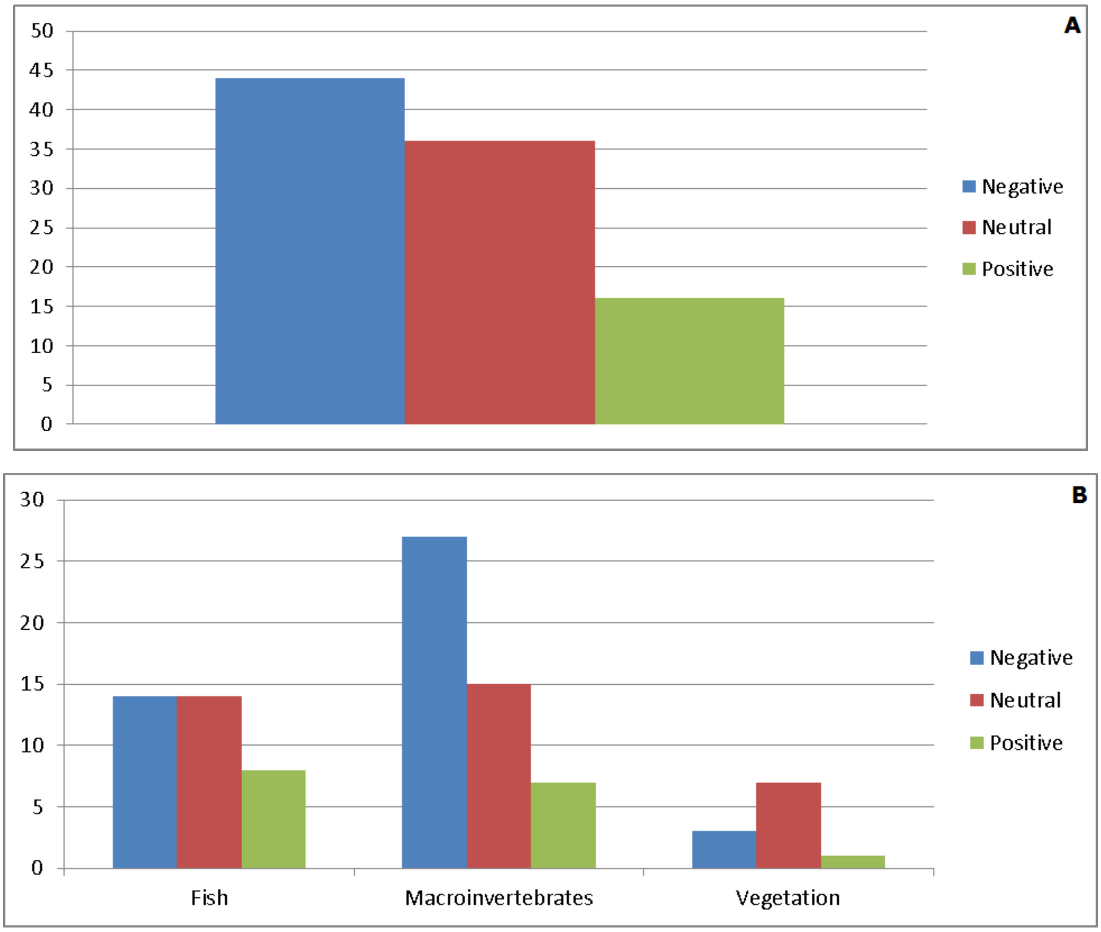


Figure 28 – Box plots for the WATCH indices: RDI and RHFI.



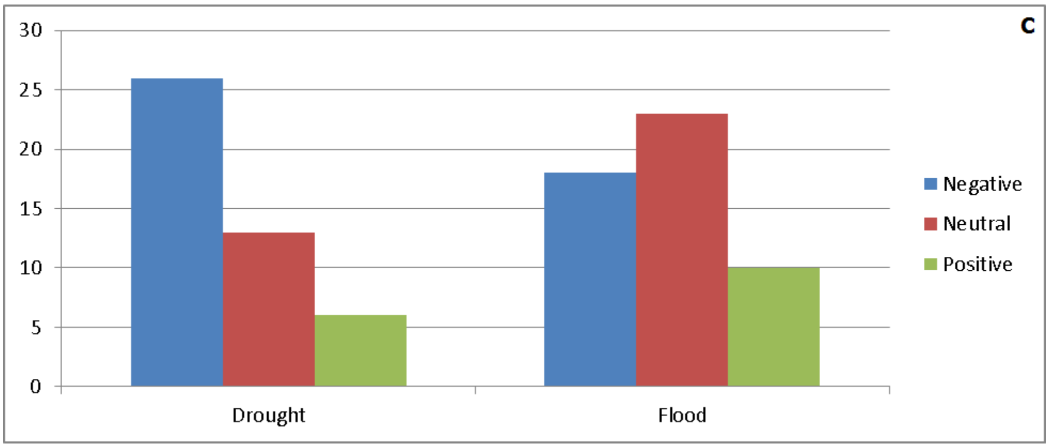


Figure 29 Directions of ecological responses: for all cases (A), and stratified by different biota (B) and extreme event types (C).

Figure 30 and Figure 31 illustrate the relationship between the hydrological indices and the ecological responses. When the cases are analysed altogether, there is no clear relationship for drought and only a weak relationship for floods. There is a stronger relationship, however, for studies investigating the impact of drought on fish. Less severe droughts are associated with more frequent neutral responses, while more severe droughts with either negative or positive, but not neutral responses.

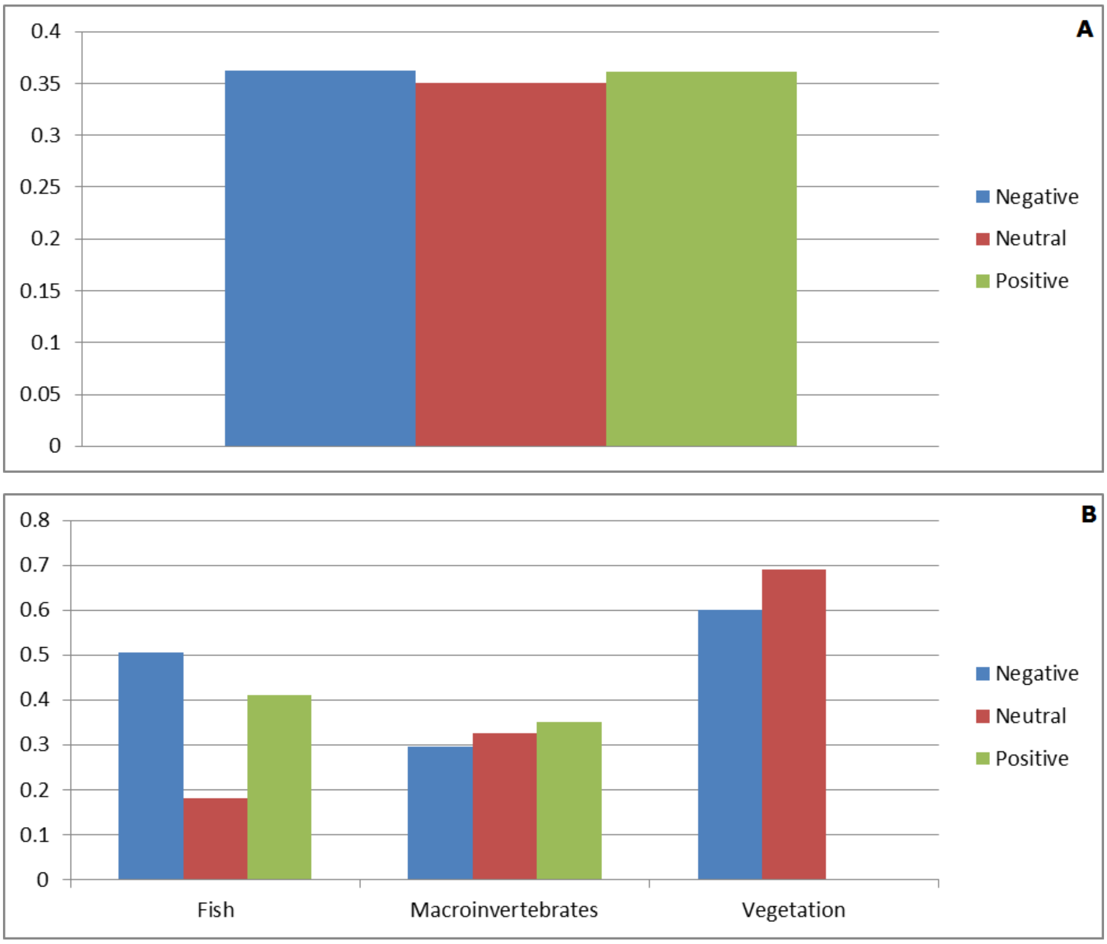


Figure 30 - Mean values of RDI stratified by different directions of ecological responses (A) and biota types (B).

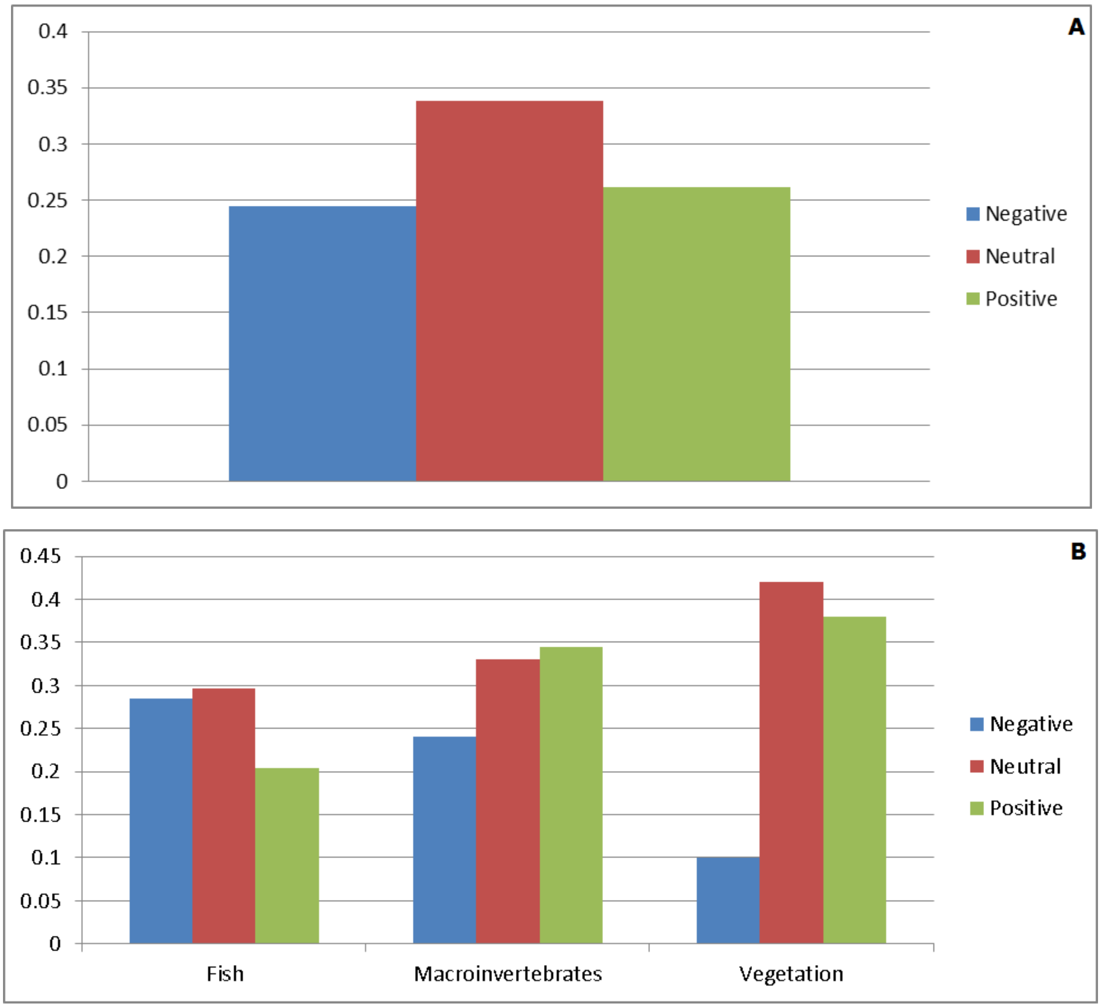


Figure 31 - Mean values of RHFI stratified by different directions of ecological responses (A) and biota types (B).

The regional analysis was carried out for three EEA biogeographical regions with the highest number of cases: Atlantic, Continental and Mediterranean (cf. Figure 25A). Figure 32 presents the same type of analysis as shown in Figure 29, but divided into the three main regions. The largest share of negative responses can be observed in the Atlantic region, whereas the Continental and Mediterranean show relatively similar proportion of response types. This can be explained mainly by a large number of studies of macroinvertebrates-drought-Atlantic region associations, in which ecological responses have been assessed as negative. As regards the subset of studies related to droughts, the Mediterranean region is the one with the highest share of neutral responses which can be explained by the fact that the fauna of intermittent streams (frequently present in this region) is expected to be both more resistant and more resilient to supra-seasonal drought than the fauna of perennial streams in any one region (Lake 2003). For the subset of studies related to floods, it can be observed that the Atlantic region is characterised by the lowest proportion of negative responses. This suggests a hypotheses that the aquatic fauna in the wet temperate region is better adapted to flood events than fauna in drier regions, although no evidence have been found in literature to support it.

The sample of vegetation studies is perhaps too small to draw conclusions, but has been presented for consistency.

Figure 33 and Figure 34 present the same type of analysis as Figure 30 and Figure 31, respectively, but divided into the three main EEA regions. Clearly the relationship between the hydrological indices and biotic response types is different when considered regionally than when data from all regions are mixed together. In the case of droughts, the main regional variability can be observed for negative responses that are associated in general with quite severe events in the Atlantic region and with less severe events in the Mediterranean region (Figure 33). A reverse relationship can be noted for the neutral responses. These observations are not easy to explain and would require more in-depth analysis. Figure 34 shows that it is the most likely that more severe high flow events cause negative ecological responses in the Atlantic region. In contrast, in the Continental region the more severe events are associated mainly with the positive responses, and in the Mediterranean region with the neutral responses. Both these statements hold true both for fish and macroinvertebrates.

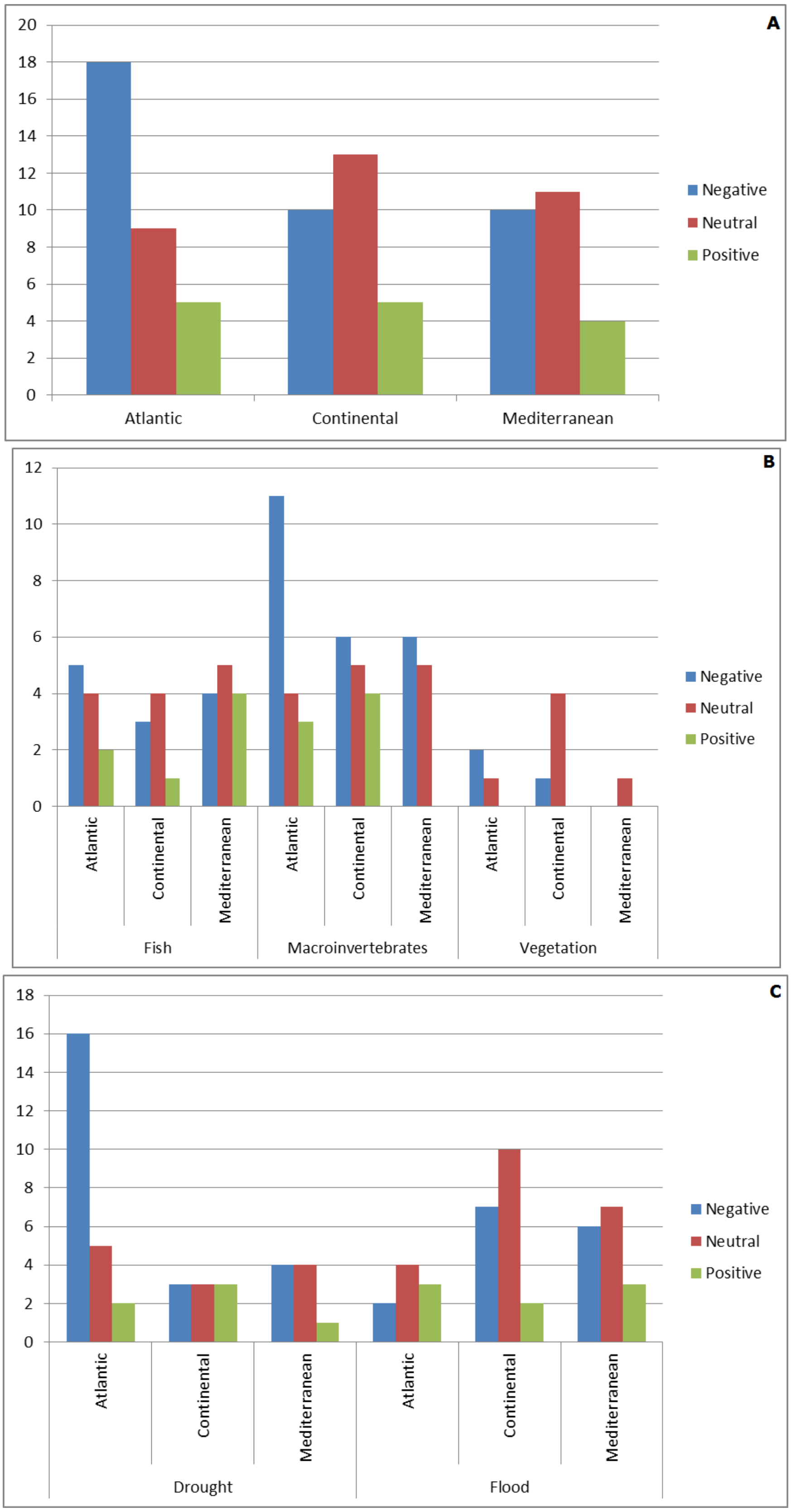


Figure 32 - Directions of ecological responses in three main EEA regions: for all cases (A), and stratified by different biota (B) and extreme event types (C).

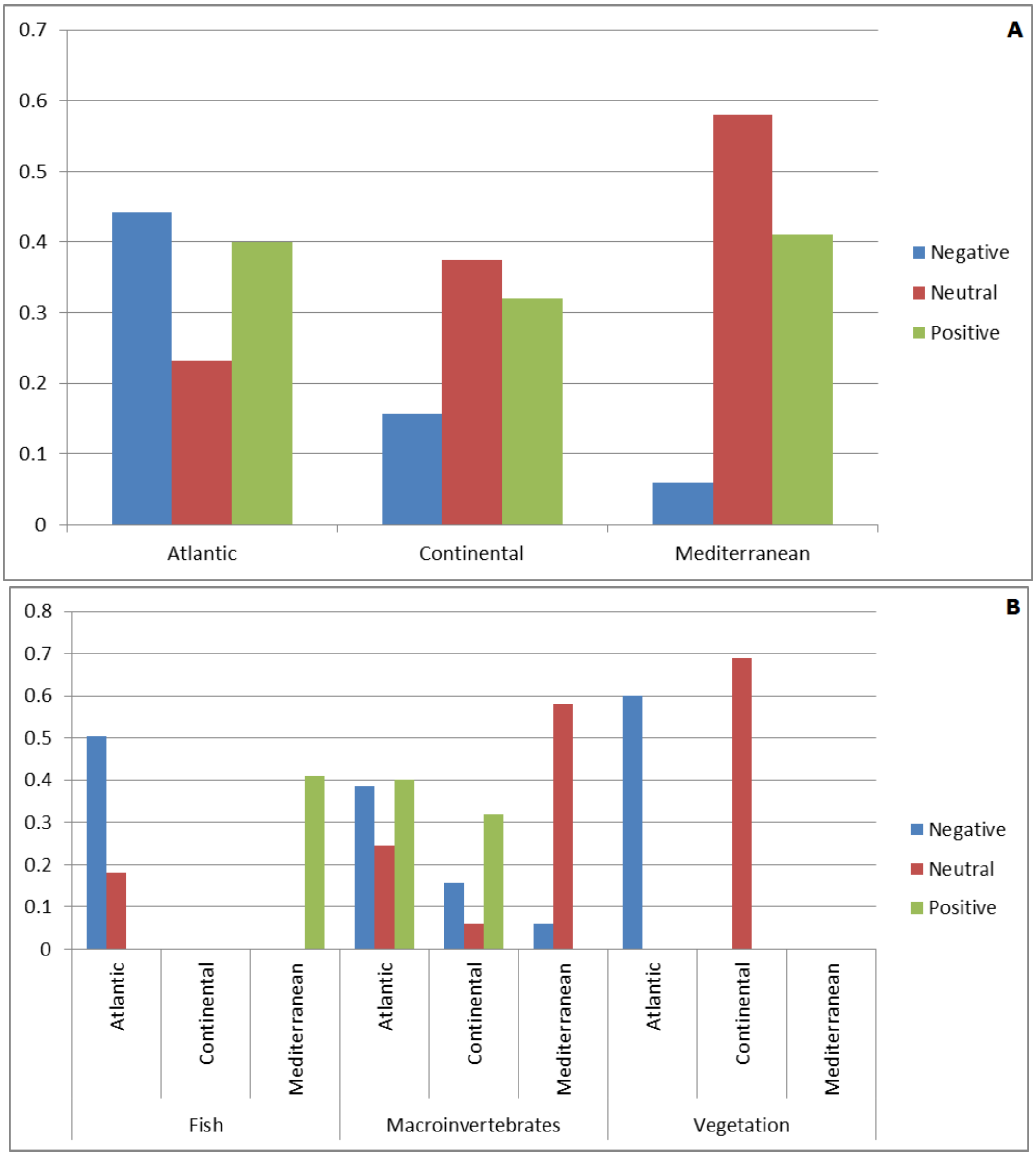


Figure 33 - Mean values of RDI for the three main EEA regions stratified by different directions of ecological responses (A) and biota types (B).

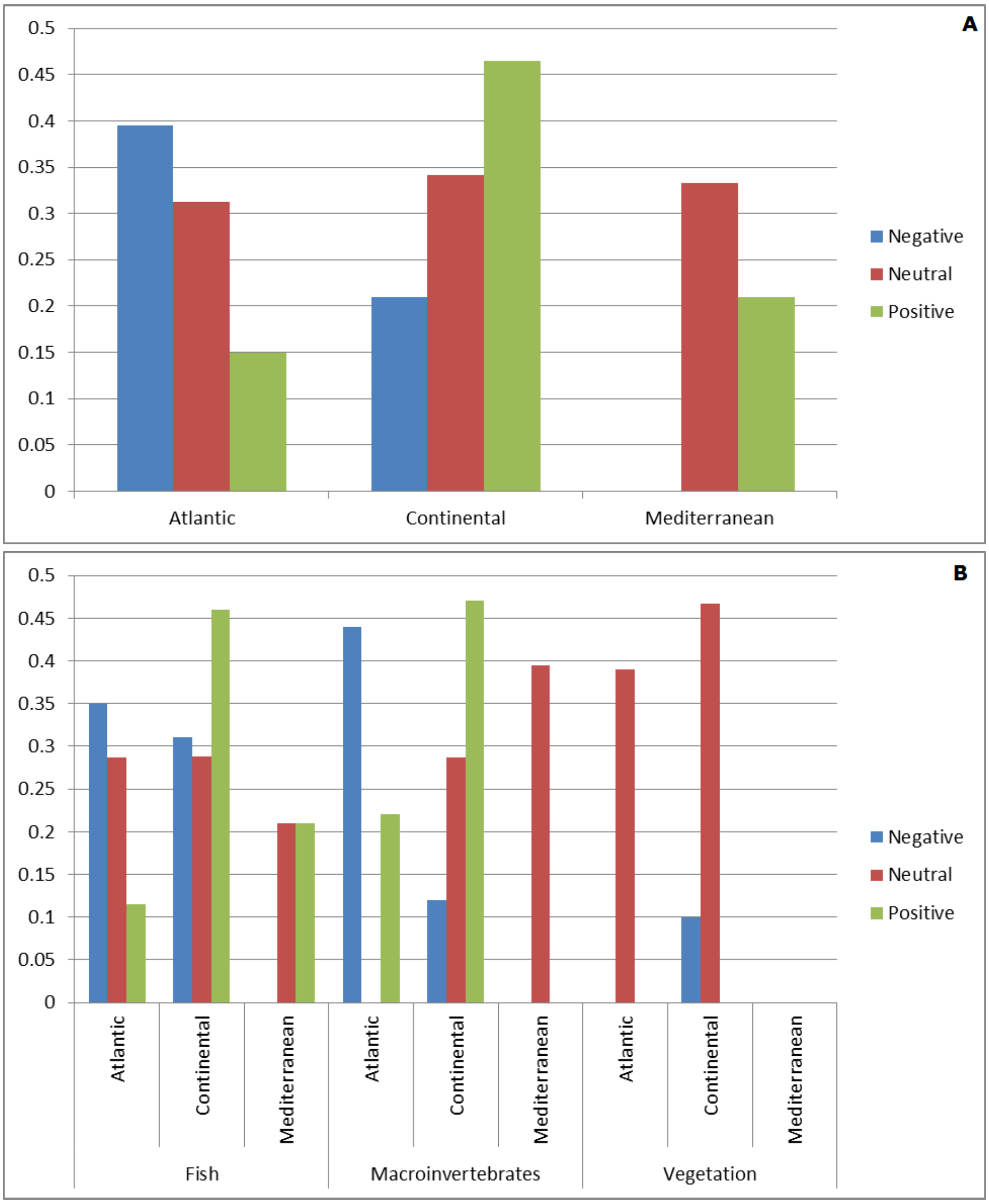


Figure 34 - Mean values of RHFI for the three main EEA regions stratified by different directions of ecological responses (A) and biota types (B).

5.2.4 Summary

The Ecological Responses to Floods and Droughts (ERFD) Catalogue developed here is a database product that can be further extended and utilized in the future, thus providing opportunities to answer various questions going beyond the scope of this deliverable. In this section we have presented example analyses, which can be summarised as follows:

- Studies investigating the effects of floods and droughts on biota analysed here spanned across whole Europe, but were the most concentrated in the Continental, Atlantic and Mediterranean biogeographical regions.

- Flood events were slightly more often studied than drought events; studies with macroinvertebrates were the most frequent and they were usually associated with droughts, whereas fish studies were usually associated with floods.
- Only 11% of all identified cases dealt with aquatic or riparian vegetation which in the light of its overall importance for hydromorphology highlighted in the part 1 of this report shows there is a considerable knowledge gap.
- Ecological responses to droughts in Europe are in general more negative than the responses to floods. However this conclusion is mainly driven by a considerable number of studies showing negative impacts of droughts on invertebrates in the Atlantic region.
- Both qualitative assessment of ecological responses with respect to different event and biota types and relationships between hydrological indices and ecological responses were more unequivocal when the analysis was made separately for different biogeographical regions than when it was made for the whole Europe. In particular some evidence was found that the Mediterranean region can be characterised by higher resilience to droughts and the Atlantic region by higher resilience to floods compared to other regions.
- The undertaken approach has certain limitations, e.g. taking into account only natural hydrological events automatically excludes large areas in which there are very few rivers with unmanaged river flows. A good example is Norway, for which no study fulfilling all selection criteria was found, since the majority of the studies on ecological responses to floods and droughts in this country deal with hydropeaking.
- In the future it would be particularly valuable to supplement the missing values of hydrological indices for all studied cases as well as to make a more detailed classification of ecological responses, e.g. referring directly to the studied ecological measures such as abundance, richness, density etc.

6. Conclusions

This concluding section refers to both parts 1 and 2 of Deliverable 2.2

The whole of Deliverable 2.2 builds upon the Hierarchical Framework developed in Deliverable 2.1 to investigate links between ecology and hydromorphology at multiple scales.

Part 1 focussed upon riparian and aquatic plants, since these are now recognised to interact with hydromorphological processes to drive the character and dynamics of rivers and their habitats. Chapters 2 and 3 developed a range of themes that relate to the rapidly developing field of fluvial biogeomorphology. Most research in this interdisciplinary field has evolved since 2000, and so it can be described as new and fast-breaking science. Chapters 2 and 3 present truly new results that demonstrate the importance of vegetation for hydromorphology. Riparian vegetation is not included as a biological quality element in the Water Framework Directive, and yet it has a fundamental influence on the hydromorphology of rivers and their floodplains, with a geographically more widespread impact than aquatic vegetation. Part 1 of this report demonstrates how vegetation interacts with hydromorphology to constrain numerous aspects of river morphology and dynamics, so providing a vital component of any river management and restoration efforts.

Nevertheless, given the brief history of this research area, it is scarcely surprising that the advances presented in part 1 also reveal a range of important research gaps. While we are confident that the conceptual model provides a useful multi-scale framework for understanding and interpreting vegetation-hydromorphology interactions in a way that can support sustainable river restoration design and management, important research gaps need to be filled before the work can be translated into a set of simple tools for river management, namely:

1. The conceptual model needs to be refined to make it more robust following its proper application to a range of European rivers. To achieve this, the application of the conceptual model must involve collection of new purpose-specific field observations. The examples presented here have synthesised pre-existing literature and field observations that were collected for many different scientific or management purposes. They have provided a 'proof of concept' and a firm basis for recommending that new purpose-specific field research is needed.
2. The thorough review of available modelling tools has also demonstrated that all of the different aspects of plant-hydromorphology interactions have received attention from modellers, although many research gaps remain. However and more importantly, most of the models only address narrow aspects of this interaction. More integrated modelling approaches are needed to better support understanding and the development of tools suitable for integrated management.
3. Although we have made significant advances in synthesising information on the natural riparian and aquatic vegetation of European rivers, and in assembling species traits that are relevant to vegetation-hydromorphology interactions, more research is

needed to add to the work that has been presented in this report. This includes both the assembly of information on native riparian and aquatic species (and their abundance) for European biogeographical regions and also the extraction of a larger set of informative species traits.

This report, which forms part 2 of Deliverable 2.2, further extends the focus on the Hierarchical Framework proposed in Deliverable 2.1, by considering its relevance to river fauna (macroinvertebrates and fish) and by incoprorating extreme hydrological events as biota-shaping phenomena.

The evidence extracted from the literature in relation to fish and macroinvertebrates in Chapter 4 demonstrates that their composition and functioning corresponds to the Hierarchical Framework of spatial scales. However, it is clear that some levels of this hierarchical structure are more relevant than others for understanding the mechanism of biological response to environmental change. In general the use of the Hierarchical Framework of spatial scales, linking macrobenthic structure and fish behaviour with functional hydromorphology, is an important tool for understanding river ecosystem organization. However, a fuller understanding could be developed if purpose-specific data sets were collected, which incorporated the full range of scales and hydromorphological phenomena into investigations of the presence and dynamics of the fauna. A particularly profitable endeavour would be to align typical hydrological, hydraulic and geomorphic units along typical river types to analyse their correspondence with the fish-based river typology (FRI).

It is also evident from the literature review and data analysis presented in Chapter 5 that both floods and droughts are phenomena that shape the structure and composition of aquatic communities. To some extent the impact of these events is moderated by the morphological characteristics of the affected river channels and their floodplains, particularly reflecting the importance of the higher complexity of naturally-functioning rivers, especially multi-thread and floodplain river systems. There is a general pattern of biological response indicating that both types of events lead to changes in aquatic community structure, limiting the organisms less adapted to the disturbance and promoting those with better adaptations. However, responses to events of different type, magnitude, intensity and duration are highly variable. Both the literature review (section 5.1) and the meta-analysis (section 5.2) suggest that a key research area remains in developing a more robust and deeper understanding of the mechanisms of biological responses to environmental changes and extreme events across different, specific, time and space scales.

Overall, this report has gone a long way towards demonstrating the importance of the Hierarchical Framework as an approach to better understanding links between hydromorphology and ecology. The Framework underpins understanding of interactions between plants and hydromorphology. We have also shown how interactions between plants and hydromorphology take on different characteristics in different biogeographical settings, leading to different spatial distributions and temporal dynamics of zones 1 to 5, and different styles of landform development within the critical interface between fluvial processes and vegetation within zones 1 to 3. These long-overlooked dynamics need serious research and management attention. Riparian vegetation needs to be more formally incorporated into the Water Framework Directive and as a fundamental component of river management and restoration design. Given its importance in relation to vegetation function, it is not surprising that the Framework has also been shown to be a useful tool in developing understanding of river fauna and their responses to extreme events.

Moving beyond the reach scale to consider the broader spatial and temporal controls on hydromorphology, ecology and their interelationships has been the central focus of this report. We hope that we have provided a useful framework for advancing this complex field, which is so important if we are to improve the management of rivers and their ecosystems.

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Annex D Responses to droughts and floods according to literature review

PublicationID	SiteID	EventDateStart	EventDateEnd	ExtremeEventType	EventDescription	BiotaType	Taxon	Response description
Argerich2004	Matarranya	2000-10-20	2000-10-20	Flood	Extraordinary flood	Macroinvertebrates	All invertebrate taxa	Decrease in density - 97,6%
Arscott2003	Tagliamento	1998-11-01	1988-11-30	Flood	The study was made during autumnal floods inter alia in November 1998	Macroinvertebrates	Insects, Polychaetes, Nematodes	Changeable in dependence to sampling site, depending to many environmental factors, generally - significant re-location of all taxa as the result of the flood
Attrill1996	Thames_up	1989-06-01	1990-10-31	Drought	In 1989 and 1990 drought conditions occurred study area, salinity of water increased because of that	Macroinvertebrates	Assellidae, Caenidae, Unionidae	The reducing freshwater flow below a critical level can have detrimental effects on the diversity of macroinvertebrate communities in certain sections of tidal rivers
Attrill1996	Thames_below	1989-08-25	1989-09-30	Drought	In 1989 and 1990 drought conditions occurred study area , the salinity of water increased	Macroinvertebrates	Assellidae, Caenidae, Unionidae	The reducing freshwater flow below a critical level can have detrimental effects on the diversity of macroinvertebrate communities in certain sections of tidal rivers
Barrat-Segretain1995	Rhone	1991-12-01	1991-12-31	Flood	Natural flood (peak discharge 2623 vs. average discharge 598 cms	Vegetation	All macrophytes comminities	The effect of the disturbances varied according to the phenology of the plants, and the macrophyte community studied was more sensitive in summer than in winter
Barrat-Segretain2007	Ain	2003-07-01	2003-08-31	Drought	The drawdown of the channel began in July 2003 and dried at least one part of the channel for 2 months. The entire channel surface was re-wattered on September 25.	Vegetation	*Elodea sp.*	Species possesses a high resilience to desiccation and that a summer drawdown would not be efficient in the control of this invasive species
Beaudou1995	Pietrapola	1989-08-01	1989-08-01	Flood	The return period of the rainfall event was 40 years and the maximum flow rate was estimated at 550 m¬ 3¬ / s	Fish	*Salmo trutta L.*	The wild population was primarily restored by the surviving individuals, particularly those from the tributaries that escaped the spate
Bernardo2003	Guadiana	1996-01-01	1996-01-31	Flood	Sampling took place from 1980 to 1999 during the water flow period	Fish	Indigenous populations of 11 species	Dramatically increasing

PublicationID	SiteID	EventDateStart	EventDateEnd	ExtremeEventType	EventDescription	BiotaType	Taxon	Response description
Bischoff2001	Oder	1997-07-10	1997-08-10	Flood	In summer 1997, a 100-year flood occurred at the River Oder. It was triggered by the cumulating effects of an exeptionally bad weather conditions.	Fish	0+fish community	Changes in fish assemblages
Bravo2001	Palancar	1995-07-01	1995-08-31	Drought	The sampling period coincided with the last years of the most severe drought experienced in the south of the Iberian Peninsula in one hundred years	Fish	All noticed species	Fish density and variety changed in proportion to the water volume
Bravo2001	Palancar	1996-11-01	1996-11-30	Flood	During some days in October and November 1995 and in April and November 1996, the stream overflowed its banks so violently that it carried away trees from the banks, bridges and irrigation channels.	Fish	All noticed species	Fish density and variety changed in proportion to the water volume
Brooker1977	Wye	1976-06-24	1976-07-02	Drought	As a result of the very low rainfall during 1976, river flows in the R. Wye were also the lowest on record (A. Tillotson, personal communication). Average flows during June and July 1976 were less than 30% of the long term average.	Fish	King salmon Salmo salar	Mass mortality of adult fish
Brooker1977	Wye	1976-06-24	1976-07-02	Drought	As a result of the very low rainfall during 1976, river flows in the R. Wye were also the lowest on record (A. Tillotson, personal communication). Average flows during June and July 1976 were less than 30% of the long term average.	Vegetation	King salmon *Salmo salar*	Decreasing numer of plant species

PublicationID	SiteID	EventDateStart	EventDateEnd	ExtremeEventType	EventDescription	BiotaType	Taxon	Response description
Bryant1999	Tay	1993-01-17	1993-01-20	Flood	The flood peak on the River Tummel was 1048 m3 sy1 and 1878 m3 sy1 at Caputh, and high water levels were maintained between the 17th and 20th of January. Flooding was induced by a rain on snow event.	Vegetation	All vegetation species	No major changes in speces composition
Bubb2002	Wharfe	2000-10-26	2000-12-05	Flood	This part of river valley is dominated by surface flow, this event is caused by river response to rapid rainfall	Fish	Signal crayfish *Pacifastacus leniusculus*	Sporadic, unpredictable
Bubb2004	Wharfe2	2002-08-01	2002-08-10	Flood	It was a midsummer flood	Fish	Pacifastacus leniusculus	Invasive potential in upstream direction
Caramujo2008	Zezere	2003-02-14	2005-02-07	Drought	The Zezere River was occured by the prolonged hydrological drought (more than 1 year)	Vegetation	Algal biofilms and meiofauna	The increase in the abundance of cyclopoid copepods, turbellarians, nematodes and chironomids in rivers during the drought
Carrel1995	Montelimar	1989-09-01	1989-10-31	Drought	The low flow period occurred from 1989 to 1993, with the most severe level in autumn 1989	Fish	*Rutilus rutilus, Alburnus alburnus, Leuciscus cephalus, Anguilla anguilla and Lepomis gibbosus*	The results prove the interest of long-term studies to appreciate variability in large river fish assemblages and the impact of river equipment.
Carrel1995	Montelimar	1993-10-01	1993-10-31	Flood	Two floods of similar magnitude occurred in October 1993 and January 1994	Fish	*Rutilus rutilus, Alburnus alburnus, Leuciscus cephalus, Anguilla anguilla and Lepomis gibbosus*	The results prove the interest of long-term studies to appreciate variability in large river fish assemblages and the impact of river equipment.
Cattaneo2001	Rhone2	1993-10-01	1993-10-31	Flood	It was the seasonal flood, caused by high rapid rainfall	Fish		Favourable effect on recruitment
Caudron2009	Borne	1987-07-01	1987-07-31	Flood	A sudden violent flood severely damaged the upstream zone and may have extirpated or greatly reduced population size	Fish	Brown trout *Salmo trutta*	Native population – resilient (also for intensive stocking of domesticated fish)
Champigneulle2003	Lac Leman	1995-12-19	1995-12-24	Flood	A high flood occurred between 24 and 31 December 1995.	Fish	*Salmo trutta L.*	Increasing mortality
Cowx1984	Afon Dulas	1976-06-25	1976-08-31	Drought	Summer drought caused by high temperatures	Fish	Salmo trutta L.	The on!y detrimental effect of the drought on the fish fauna was the elimination of the 1976 year class of young salmon

PublicationID	SiteID	EventDateStart	EventDateEnd	ExtremeEventType	EventDescription	BiotaType	Taxon	Response description
Cowx1984	Afon Dulas	1976-06-25	1976-08-31	Drought	Summer drought caused by high temperatures	Macroinvertebrates	All the invertebrate community	An initial reduction in abundance during the drought and a change in community structure in the following year were observed
Dumnicka2005	ŁękukWielki	1997-10-01	1999-09-01	Drought	The streans dry out time to time during the summer and winter	Macroinvertebrates	Polychaetes	Rapid increase in density just after the drought, later gradual decrease
Elliott2000	Wilfin Beck	1976-07-01	1976-07-11	Drought	Some characteristics of the pools were recorded every day from 1–14 July in the two drought years (1976, 1983) and in two non-drought years (1977, 1985).	Fish	Brown trout Salmo trutta	Looking for pools as the refugia
Elliott2000	Wilfin Beck	1983-07-11	1983-07-14	Drought	Some characteristics of the pools were recorded every day from 1–14 July in the two drought years (1976, 1983) and in two non-drought years (1977, 1985).	Fish	Brown trout Salmo trutta	Looking for pools as the refugia
Extence1981	Roding	1976-05-01	1976-10-31	Drought	During the summer months of 1976 after a winter of abnormally low rainfall, the continuingloss of water from fresh water ecosystems became critical in many parts of the country	Macroinvertebrates	Many invertebrate groups	The majority of the communities – increase in density. Caddisflies and snails – decrease in density
Fenoglio2006	Po	2004-08-10	2004-12-01	Drought	Water level below the hyporheic traps installed in the river bed. Drought length varies along the longitudinal gradient: water present in the streambed from 2-3 months to 12 months.	Macroinvertebrates	*Agabus paludosus*	The need for changes in habitat
Fenoglio2006	Po	2004-08-10	2004-12-01	Drought	Water level below the hyporheic traps installed in the river bed. Drought length varies along the longitudinal gradient: water present in the streambed from 2-3 months to 12 months.	Macroinvertebrates	*Agabus paludosus*	The need for changes in habitat
Fenoglio2007	Po2	2004-08-05	2004-10-05	Drought	In this particular case the period drought was occurred in the site	Macroinvertebrates	Dytiscidae beetles	Larvae and adults 70-90 cm below surface

PublicationID	SiteID	EventDateStart	EventDateEnd	ExtremeEventType	EventDescription	BiotaType	Taxon	Response description
Fonnesu2005	Pula	2001-08-01	2002-10-30	Drought	Seasonal drought occured the area during summer-autumn time	Macroinvertebrates	All invertebrate taxa	Rapid changes in biocenosis and peculiar communities, the authors stress, that the droughts and floods are common in Mediterranean area and take place by turns
Gaudes2010	Fuirosos	2003-07-01	2003-07-30	Drought	It was summer drought when the stream was totally dry	Macroinvertebrates	Copepods, Namatodes, Gastropods, Rotifers	Special traits to adapt to hydrological perturbations, abundance and resilience higher in the upstream reach. Low-order reaches- important as refugia- may eventually repopulate downstream reaches
Gaudes2010	Fuirosos	2003-11-30	2003-12-13	Flood	The flood occurred this are was a result of high precipitation	Macroinvertebrates	Copepods, Namatodes, Gastropods, Rotifers	Special traits to adapt to hydrological perturbations, abundance and resilience higher in the upstream reach. Low-order reaches- important as refugia- may eventually repopulate downstream reaches
Gaudes2010	Fuirosos	2004-05-20	2004-05-25	Flood	The flood occurred the area during late spring was a result of high precipitation	Macroinvertebrates	Copepods, Namatodes, Gastropods, Rotifers	Special traits to adapt to hydrological perturbations, abundance and resilience higher in the upstream reach. Low-order reaches- important as refugia- may eventually repopulate downstream reaches
Gerisch2012	Elbe2	2002-08-01	2002-08-30	Flood	In the summer of 2002, unpredictable severe precipitation led to the highest flooding ever recorded along this river	Macroinvertebrates	Ground beetles	Species richness decreased strongly immediately after the flood but reached pre-flood values 2 years later. Persistent shifts in species composition and abundance.
Godinho2000	Guadiana2	1994-01-01	1994-06-30	Drought	The year of 1994 culminated a succession of extremely dry years, beginning in 1992	Fish	Fish community	Selected environmental variables: – depth, width, substrate heterogeneity and altitude – have been determined to be important correlates of fish assemblage
Grzybkowska1990	Grabia	1985-08-05	1985-08-20	Flood	The one of the highest water level during 20-years period, water washed out organic matter from the bottom	Macroinvertebrates	Chironomids	The number of the chironomids species in coarse sediment highest in the spring, in sand – in summer. Decreasing in numbers in autumn and winter.

PublicationID	SiteID	EventDateStart	EventDateEnd	ExtremeEventType	EventDescription	BiotaType	Taxon	Response description
Grzybkowska1996	Widawka	1985-08-05	1985-08-20	Flood	The discharge in August 1985 was the highest since 1955 and resulted in significant erosion and rearrangement of streambed material	Macroinvertebrates	Chironomid community	More mosaic habitats resulted in higher densities. Flooding affected the distribution and abundance of the chironomid assemblages
Henry1994	Miribel	1991-12-22	1991-12-23	Flood	It was winter major flood with discharge 2623 m3/s	Vegetation	All vegetation communities	Terrestial plants progressively replaced aquatic ones that dried up
Hering2004	Isar	1999-05-17	1999-05-27	Flood	In May 1999, the Isar floodplain was affected by a severe flood	Macroinvertebrates	Land beetles (Carabidae) connected with the banks	Lowest density one month after the flood, 2 months later – highest from 1993
Hering2004	Isar	1999-05-17	1999-05-27	Flood	In May 1999, the Isar floodplain was affected by a severe flood	Vegetation	Almost all invertebrate taxa	No significant changes
Ilg2008	Steckby3	2002-08-01	2002-08-30	Flood	In the summer of 2002, unpredictable severe precipitation led to the highest flooding ever recorded along this river	Vegetation	All plant species	The efficiency of resistance and resilience strategies is widely dependent on the mode of adaptation
Ilg2009	Elbe2	2002-08-01	2002-08-30	Flood	In August 2002, they were affected by the highest Elbe flood ever recorded, with a statistical recurrence interval of 168 years, and were inundated for at least two weeks.	Macroinvertebrates	Land beetles (Carabidae) connected with the banks	Increase in diversity and density in numbers during the first year after the flood, water species sighting. Later gradually return to the previous state.
Jansson2005	Vindel	1999-04-20	1999-04-26	Flood	It was seasonal flood occured this area after the rainfall	Vegetation	Riparian plant species	Riparian plant communities may receive a comparatively large proportion of their seeds by long-distance dispersal by the water
Jurajda2006	Morava	1997-07-01	1997-07-31	Flood	In early July 1997 discharge of the lower R. Morava increased rapidly and exceeded 2000% of the long-term average (45 m3/s). A discharge of more than 1000% of the average lasted for more than 20 days. Dikes were not overtopped	Fish	Pelagic species (e.g. bleak and roach) and benthic species (e.g. barbell)	The largest decline. Decrease in abundance of one-year-old individuals
Ledger2001	Lone Oak	1995-04-01	1995-08-31	Drought	During the spring and early summer stream discharge fell continuously leaving the surface bed sediments dry	Macroinvertebrates	Various macroinvertebrate taxa	Decreasing in numbers, but later recolonisation to the previous level of density and abundance

PublicationID	SiteID	EventDateStart	EventDateEnd	ExtremeEventType	EventDescription	BiotaType	Taxon	Response description
Lobon-Cervia1990	Chabatchos	1986-07-15	1986-08-01	Drought	It was a drought in summer time caused by high temperature	Fish	*Anguilla Anguilla L.*	No negative influence on eels
Lobon-Cervia1996	Esva	1993-12-26	1994-01-10	Flood	The flood was caused by 5h heavy rain in December 26, water level was 4 times higher than	Fish	Brown trout, Atlantic salmon and European eel	No evidences of negative effect
Lobon-Cervia2009	RioChaballos	2003-11-01	2003-11-30	Flood	It was one of the flash floods	Fish	Brown trout (Salmo trutta)	Decreasing in numbers – quick recovery
Lojkasek2005	Olse	1997-07-06	1997-07-10	Flood	In July 1997, an extremely high amount of precipitation fell down on the territory of the Czech Republic (Moravia, Silesia). Consequently, extreme floods were experienced in most streams in the catchment basin areas of the Oder	Fish	Brown trout Salmo trutta and grayling Thymmalus thymmalus	Increasing in numbers, in the case of grayling more pronounced decrease in the years after the floods
Lojkasek2005	Opava	1997-07-06	1997-07-10	Flood	In July 1997, an extremely high amount of precipitation fell down on the territory of the Czech Republic (Moravia, Silesia). Consequently, extreme floods were experienced in most streams in the catchment basin areas of the Oder	Fish	Brown trout Salmo trutta and grayling Thymmalus thymmalus	Increasing in numbers, in the case of grayling more pronounced decrease in the years after the floods
Lojkasek2005	Osoblaha	1997-07-06	1997-07-10	Flood	In July 1997, an extremely high amount of precipitation fell down on the territory of the Czech Republic (Moravia, Silesia). Consequently, extreme floods were experienced in most streams in the catchment basin areas of the Oder	Fish	Brown trout Salmo trutta and grayling Thymmalus thymmalus	No negative impact

PublicationID	SiteID	EventDateStart	EventDateEnd	ExtremeEventType	EventDescription	BiotaType	Taxon	Response description
Lojkasek2005	CernyPotok	1997-07-06	1997-07-10	Flood	In July 1997, an extremely high amount of precipitation fell down on the territory of the Czech Republic (Moravia, Silesia). Consequently, extreme floods were experienced in most streams in the catchment basin areas of the Oder	Fish	Brown trout Salmo trutta and grayling Thymmalus thymmalus	Catches of the species of Salmo trutta and Thymallus thymallus in 1997 considerably increased
Lojkasek2005	StredniOpava	1997-07-06	1997-07-10	Flood	In July 1997, an extremely high amount of precipitation fell down on the territory of the Czech Republic (Moravia, Silesia). Consequently, extreme floods were experienced in most streams in the catchment basin areas of the Oder	Fish	Brown trout *Salmo trutta* and grayling *Thymmalus thymmalus*	Thymallus thymallus experienced a more pronounced decrease in the years after the floods
Lusk2004	Kyjowka	1997-07-01	1997-08-31	Flood	The form of the flood (caused by high precipitation) occurred the area was distinctly affected by the channelization of the rivers	Fish	*Aspius aspius, Leuciscus idus, Alburnus alburnus, Abramis ballerus, Carassius auratus*	Increase of abundance of species
Magalhaes2007	Torgal	1994-10-01	1994-12-30	Drought	It was the culmination drought event after long wet time	Fish	Fish assembalges	Increasing in assemblages variability, little changes in species richness, significant variation in individual species abundance
Martinho2007	Mondego2	2004-04-01	2005-11-30	Drought	The extreme drought occured this area, the level of precipitation was far below average	Fish	42 species with estuarine residents and nursery species dominating the community	Depletion of the freshwater species and an increase in marine adventitious
Masters2002	Frome	2000-11-30	2000-12-30	Flood	Flood occurred the area was caused by high precipitation	Fish	Pike Esox lucius	Individual variation amongst fish for the habitat type selected
Matthaei1997	Aachsage	1994-07-04	1994-07-09	Flood	The flood event was caused by high precipitation during the summer time	Macroinvertebrates	Various macroinvertebrate taxa	The reduction in the total number of individuals and the dominant taxa, the recolonization pattern of *Rhitrogena* spp., *Leuctra* spp., Hydracarina, Chironomidae, *Baetis* spp. , Simuliidae, Pentaneurini and *Coryoneura /Theinemanniella* spp. Showed a distinct lag phase after the flood

PublicationID	SiteID	EventDateStart	EventDateEnd	ExtremeEventType	EventDescription	BiotaType	Taxon	Response description
Meyer2000	Sauer	1996-04-12	1996-06-30	Drought	The Sauer has a period of low flow from May to September, when parts of the temporary sections dry up completely every year	Macroinvertebrates	All invertebrate fauna	On the constant flowing reaches – fauna typical for mountain and submountain streams, on the periodic ones – the species of the strategies adopted to the periodic water bodies, the communities dominated by caddisflies.
Morais2004	Grandola	2002-04-10	2002-04-12	Flood	Flood caused by the heavy storms	Macroinvertebrates	Various macroinvertebrate taxa	Significant, but various and depending to the taxa and peculiar situation changes in the species richness and percentages.
Morrison1990	Loch Ard	1984-06-01	1984-08-19	Drought	It was the longest dry summer occurred on this area	Macroinvertebrates	Many benthic invertebrates species	Research showed significant difference in population size for a few species
MothIversen1978	OrnedBaek	1976-10-10	1976-10-24	Drought	The expanding use of ground and stream water for drinking and agricultural purposes cause drying of streams and have an influence on macroinvertebrates.	Macroinvertebrates	All invertebrate fauna	The effect depending on the life cycle of peculiar taxa. Just after the drought a lot of new species have appeared, but – except *Asellus aquaticus*.
MothIversen1978	Ravnstrup	1976-10-10	1976-10-24	Drought	The expanding use of ground and stream water for drinking and agricultural purposes cause drying of streams and have an influence on macroinvertebrates.	Macroinvertebrates	All invertebrate fauna	The effect depending on the life cycle of peculiar taxa. Just after the drought a lot of new species have appeared, but – except *Asellus aquaticus*.
MothIversen1978	MillingBaek	1976-10-10	1976-10-24	Drought	The expanding use of ground and stream water for drinking and agricultural purposes cause the drying of streams and have an influence on macroinvertebrates.	Macroinvertebrates	All invertebrate fauna	The effect depending on the life cycle of peculiar taxa. Just after the drought a lot of new species have appeared, but – except *Asellus aquaticus*.
Munoz2003	Riera Major	1992-07-01	1992-09-30	Drought	It was natural drought occurred an intermittent stream during the summer	Macroinvertebrates	Various invertebrate taxa	In both streams- different seasonal distribution of the biomass of different functional groups (basic aim of the study)
Ortega1991	Rambla del Moro	1986-10-07	1986-10-07	Flood	The channel width during flood ranged between 1.5 and 3.6 m and the width between 5 and 60 cm	Macroinvertebrates	Invertebrates community	High community resilience because the community structure recovers a month later

PublicationID	SiteID	EventDateStart	EventDateEnd	ExtremeEventType	EventDescription	BiotaType	Taxon	Response description
Otermin2002	Jergueron	1995-08-15	1995-11-15	Drought	The stream dried up for 3 months, water flow was reestablished after the autumn rains	Macroinvertebrates	Macroinvertebrate community	The species richness very low. Chironomidae, Ceratopogonidae, Odonata, Oligochaeta and Mollusca recorded in the streambed. Non-flying taxa dominant in density and biomass just after the beginning of re-colonisation. Taxa hatching in winter - *Capnioneura* and Glossosomatidae – less affected by the drought. Significant increasing in density and biomass over time after the drought.
Pires1999	Guadiana3	1996-01-01	1996-03-01	Flood	Several natural floods occurred at the beginning of the year	Fish	Cyprinids fishes	Intense aggregation of fish and possible competition for food or/and space.
Pires2008	Odelouca	1997-10-26	1997-10-27	Flood	On October 1997 a severe flash flood occurred this area as a result of abnormal rainfall episode of 274,7mm in 1,5h	Fish	Native fish assemblages	Little disruptive effect on the overall structure , although may partially influence population dynamics for some species
Plum2005	Elbe	2003-06-11	2003-07-19	Drought	Compared to Bremen, the Gorleben region recorded a lower annual precipitation in both years of study and more sun hours in 2003	Macroinvertebrates	Earthworms from Lumbricidae and Enchytraeidae families	Decrease in number of species
Plum2005	Wumme	2003-06-10	2003-07-15	Drought	The exceptional dry spring and summer of 2003 subjected the region to another hydrological extreme.	Macroinvertebrates	Earthworms from Lumbricidae and Enchytraeidae families	The number of taxa was stable
Plum2005	Wumme	2002-07-20	2002-08-21	Flood	A summer flood in 2002 (July 20–August 21 at air temperatures of 20–30 C)	Macroinvertebrates	Earthworms from Lumbricidae and Enchytraeidae families	Summer flood eliminated all annelids in turf soil but drought – in gley one. The drought reduced the number of earthworms mostly in July, when Enchytreidae reached the peak of density.
Plum2005	Elbe	2002-08-18	2002-08-18	Flood	Heavy rains on the remote catchments in the first 2 weeks of August 2002 caused an enormous flood that reached the Gorleben site downstream on August 18 and stayed until September 11	Macroinvertebrates	Earthworms from Lumbricidae and Enchytraeidae families	Summer flood eliminated all annelids in turf soil but drought – in gley one. The drought reduced the number of earthworms mostly in July, when Enchytreidae reached the peak of density.

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Plum2005	Elbe	2002-08-18	2002-09-11	Flood	Heavy rains on the remote catchments in the first 2 weeks of August 2002 caused an enormous flood that reached the Gorleben site downstream on August 18 and stayed until September 11	Macroinvertebrates	Earthworms from Lumbricidae and Enchytraeidae families	Summer flood eliminated all annelids in turf soil but drought – in gley one. The drought reduced the number of earthworms mostly in July, when Enchytreidae reached the peak of density.
Pupilli2003	Vallderroures	2000-10-25	2000-10-30	Flood	Intense meteorological events caused extraordinary flood, the greatest of the last 500 years	Macroinvertebrates	Mayflies and stoneflies	Decreasing in numbers by 97%, change of diet for detritus with diatoms.
Pupilli2003	Parrizai	2000-10-25	2000-10-30	Flood	Intense meteorological events caused extraordinary flood, the greatest of the last 500 years	Macroinvertebrates	Mayflies and stoneflies	Decreasing in numbers by 97%, change of diet for detritus with diatoms.
Reichard2004	Jihlava	1999-07-08	1999-07-09	Flood	In 1999 the elevated river discharge in the summer was studied	Fish	Young of – the – year cyprinid fishes	Increasing in abundance of drifting fish of peculiar age, size and taxa effected by increasing in current velocity and water turbidity
Reznickova2013	Granicky	2002-07-06	2002-07-15	Drought	It was the natural extreme event occurred the area which was not typical for this region in the past	Macroinvertebrates	Benthic macroinvertebrates assembleges	Lower numer of taxa tan in permanent stream
Reznickova2013	Klaperuv	2002-07-06	2002-07-15	Drought	It was the natural extreme event occurred the area which was not typical for this region in the past	Macroinvertebrates	Benthic macroinvertebrates assembleges	Number of taca and diversity without changes
Ruegg2004	Macun Lake	2003-07-01	2003-08-31	Drought	Summer 2003 was exceptionally hot and dry with most of Switzerland in drought. Drought had a major influence on temporary streams in the study area	Macroinvertebrates	Macroinvertebrate assemblages	Rapid increase in numbers of *Crenobia alpine*/ faster development and growth of the simuliid *Prosimulium latimucro*.
Silva-Santos2004	Mondego4	2001-01-26	2001-01-27	Flood	The flood occured the area had big impact on local habitats	Fish	Fish community	High resistance to the changes
Silva-Santos2004	Mondego3	2001-01-26	2001-01-27	Flood	The flood occured the area had big impact on local habitats	Macroinvertebrates	Macroinvertebrate communities	High resistance to the changes, inter-annual differences obscured by the seasonal ones
Strausz2007	Mitterwasser	2002-06-01	2002-06-30	Flood	The extreme flood event occurred this area was caused by high precipitation	Vegetation	Aquatic macrophytes	A pronounced change in species composition was noticed

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Tetzlaff2005	Ginrock Burn	1995-12-20	1996-01-05	Flood	It is natural flood event occurred this area during the winter season	Fish	Juvenile and spawning Atlantic salmon	Complex relationship with hydrological variability with marked inter-annuals contrasts
Titus1992	Tullviksbacken	1988-05-01	1988-05-31	Drought	The drought was caused by very low precipitation	Fish	Migratory brown trout Salmo trutta	Variable fry mortality following emergence in early summer
Wood1999	LittleStour	1989-01-01	1992-08-10	Drought	Drought occurred on the area from 1988 to 1992, ground water level declined, large areas of the river were covered by sediments because of low water flow	Macroinvertebrates	Macroinvertebrates	Just a few taxa elimination, what suggests the presence of the refuges.
Wood1999	LittleStour	1995-04-01	1995-08-31	Drought	In 1995 there was summer drought caused by deficit of rainfall, however it had no perceptible impact on river flow in the Little Stour due to high groundwater levels.	Macroinvertebrates	Macroinvertebrates	Few taxa were eliminated as a result of the drought
Wood2004	LittleStour	1992-01-01	1992-10-31	Drought	It was supra-seasonal drought event which lead to the desiccation of two historically perennial reaches	Macroinvertebrates	All the community with especially attention to *Gammarus pulex*	Extremely low community abundance, also in the case of *Gammarus pulex*, recovery after 2 years
Wood2004	LittleStour	1996-01-01	1997-12-31	Drought	It was supra-seasonal drought event which lead to the desiccation of two historically perennial reaches	Macroinvertebrates	All the community with especially attention to *Gammarus pulex*	Extremely low community abundance, also in the case of *Gammarus pulex*, recovery after 2 years
Wright1999	Lambourn	1973-10-01	1973-11-30	Flood	Several small floods occurred this area before major flood in 1976	Macroinvertebrates	All the invertebrate community	No evidence of loss of species richness, some biotopes supported unusually high densities of macroinvertebrates from a limited number of families
Wright2002	Kennet2	1991-12-01	1992-01-31	Drought	It was a protracted flood occurring the area approx. for 2 years	Macroinvertebrates	All the invertebrate community	No evidences of major loss of family richness. Following the end of the drought many invertebrates showed a rapid response to the new conditions, assemblages reverted to those expected in a fast-flowing chalk stream
Wright2002	Kennet2	1996-12-01	1997-01-31	Drought	It was major flood occurred this area which was proceeded by protracted floods in previous years	Vegetation	*Ranunculus*	No evidences of major loss of family richness. Following the end of the drought many invertebrates showed a rapid response to the new conditions, assemblages reverted to those expected in a fast-flowing chalk stream

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Wright2004	Kennet	1997-03-01	1997-05-30	Drought	It was a major drought in 1997 in the chalk stream	Macroinvertebrates	Macroinvertebrate assemblages	The recent high discharge regimes have had no immediate detrimental consequences for the macroinvertebrate assemblages
Wright2004	Kennet	2001-03-01	2001-05-30	Flood	The wet period resulting in sustained high groundwater levels and consequently very high discharge in each catchment	Macroinvertebrates	Macroinvertebrate assemblages	Major changes took place in family composition and abundance