The role of floods and droughts on riverine ecosystems under a changing climate

Piotr Parasiewicz[1,2], Elise L.King[3], J. Angus Webb[3], Mikołaj Piniewski[2], Claudio Comoglio[4], Christian Wolter[5], Anthonie D. Buijse[6], David Bjerklie[8], Paolo Vezza[4], Andreas Melcher[7], Katarzyna Suska[1]

[1]The Stanisław Sakowicz Inland Fisheries Institute, ul. Oczapowskiego 10, 10-719 Olsztyn 4, Poland

[2]Department of Hydraulic Engineering, Warsaw University of Life Sciences, Nowoursynowska 159, Warsaw, Poland

[3] Environmental Hydrology and Water Resources, Department of Infrastructure Engineering, The University of Melbourne, Parkville, Victoria, 3010, Australia

[4] Turin Polytechnic, Corso Duca degli Abruzzi 24, c/o DITAG, 10129 Torino, Italy

[5] Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310

12587 Berlin, Germany

[6] Deltares, Daltonlaan 600, 3584 BK Utrecht, Netherlands

[7] Institute of Hydrobiology and Aquatic Ecosystem Management, University of Natural Resources and Life Sciences, Max Emanuelstrasse 17, 1180 Vienna, Austria

8 Retired, U.S. Geological Survey New England Water Science Center, Connecticut Office 101 Pitkin Street East Hartford, CT 06108 United States .

ABSTRACT

Floods and droughts are key driving forces shaping aquatic ecosystems. Climate change may alter key attributes of these events and consequently health and distribution of aquatic flora and fauna. Improved knowledge of natural biological responses to different types of floods and droughts in rivers would allow us to better predict the ecological consequences of climate change-induced flow alterations. This review highlights that in unmodified ecosystems, the intensity and direction of biological impacts of floods and droughts vary, but the overall consequence is an increase in biological diversity and ecosystem health. To predict impact of climate change, physical metrics allowing to quantitatively link the physical disturbance attributes to the directions and intensities of biological impacts is needed. The link between the physical change and character of biological response is provided by the frequency of occurrence of the river wave characteristic – i.e. the event's predictability. The severity of impacts of floods is largely related to river wave amplitude (flood magnitude), and of droughts to river wave length (drought duration). Presented analysis of three rivers in Poland demonstrates how river wave characteristics for floods and droughts can be captured with flow duration statistics, and with help of habitat models and Uniform Continuous Under Threshold duration techniques, respectively.

Kewords: river wave concept, biological response, extreme events, disturbance, hydromorphology, climate change, river ecosystems, river floods, river droughts, warming.

INTRODUCTION

Global climate change is expected to modify patterns of hydrological events in many regions of the world (Glaser et al. 2010, Garner et al. 2015, Blöschl et al., 2017, Bormann et al. 2017, Markovic et al. 2017), affecting water temperature (Markovic et al. 2013, Van Vliet et al. 2013), and changing the temporal distribution of river flows (Blöschl et al. 2017). Since flow is considered a master variable shaping riverine ecosystems, such changes are expected to cause substantial shifts in the composition of aquatic communities (Guse et al. 2015, Rolls et al. 2016). This could lead to massive extinctions or to the creation of new traits and adaptations (Myers et al. 2017). The changes may vary depending on climate change magnitude and geographic location.

Understanding functional relationships between flow patterns and biological consequences is of the outmost importance for planning adaptation measures to climate change and for sustainable river management. Defining elements of the hydrological regime directly responsible for shifts in community composition is necessary. Subsequently, the attributes determining the direction and magnitude of the shift can be identified.

It is widely recognized that extreme events such as floods and droughts are a major driving force behind the composition of aquatic biotas (e.g. Poff et al. 2007, Sukhodolov et al. 2009, Wolter et al. 2016, Poff 2018). However, not all floods and droughts are the same, and therefore different events have different consequences. Knowledge of the directions and intensities of natural biological responses to different types of floods and droughts would allow to better understand and predict the consequences of natural and anthropogenic alterations.

To be precise in predictions useful for climate adaptation planning it is necessary to identify the appropriate quantitative metrics of disturbance that correlate with biological responses. Thus, the role that floods and droughts play in biological cycles needs to be better understood. Specifically, the following questions need to be answered:

- What are the functional mechanisms between physical patterns and biological response?
- Which attributes of floods and droughts are most closely related to population shaping phenomena?
- Which of these attributes are most sensitive to climate change effects?

While there is a substantial body of literature relating to various aspects of floods and droughts, the information is disjointed and not synthesized in a fashion that allows to fully understand the driving forces and mechanisms leading to biological responses. Therefore, the purpose of this paper is to:

- provide a systematic overview of the topic based on a review of the recent literature;
- identify practical, quantitative metrics that may be used to estimate the climate-induced modifications of flow patterns that determine biological response.

The paper concludes with an application of the identified metrics in three case studies for rivers in Poland.

FLOODS AND DROUGHTS AS ECOLOGICAL DISTURBANCE PROCESSES

For the ecology of a system, floods and droughts are considered physical disturbances, i.e. stochastic events forcing normal system environmental conditions substantially away from the mean (Stanford and Ward, 1983, Puckridge et al. 1998, Death et al. 2015, Fuller et al. 2019). Physical disturbance is a natural component of aquatic ecosystems, and aquatic biotas are adapted to deal with these disturbances (Resh et al., 1988; Fisher & Grimm, 1991; Lake, 2000, Lytle & Poff 2004, Van Looy et al. 2019).

Lake (2000) described three types of disturbance: pulse, press and ramp, which trigger three different processes that alter populations. A pulse disturbance causes an instantaneous alteration in animal or plant densities and possibly diversity, while a press disturbance causes a sustained change in abundance or composition. Ramps have been defined as disturbances that increase in strength (and often spatial extent) over time (Lake, 2000). Obviously, these definitions refer to a temporal scale experienced by individual organisms, and for aquatic organisms at the spatial scale of the reach. At this scale, floods are most often pulse or press disturbances, and droughts tend to be ramps. At coarser temporal scales all disturbances may be considered as pulses (Poff, 1992; Lake, 2003).

HABITAT CHANGES

Functionally, disturbance changes the quantity and quality of habitat available, which can directly modify community composition as well as affect biotic interactions (Fisher et al., 1982; Grossman et al., 1982, 1998; Reice, 1985; Frissel et al. 1986, Junk 2005, Parasiewicz et al., 2012, Winemiller et al. 2014, Gurnell et al. 2016, Leigh & Datry 2017). 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 persist after the event for a considerable time (Pearsons et al. 1992, Bork & Kranz 2008, Death et al. 2015, Leigh & Datry 2017).

HABITAT CHANGES CAUSED BY FLOODS

Floods affect habitat elements such as stream substrate composition, stability, refugia, river channel cross-section and planform morphology, and the flow regime (Poff, 1992; 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, Pearsons et al. 1992, Wetter et al. 2010, Stolz et al. 2013, Herget et al. 2015). The effects of flooding may vary from minor geomorphological changes caused by small spates or freshets, to alteration of the entire structure of the stream channel caused by extended, powerful high discharge events (Costa and O'Connor, 1995; Bork & Kranz 2008, Dotterweich 2008, Hauer & Habersack 2009). Wolman and Miller (1960) showed that floods of bankfull discharge cause most geomorphological change because they have significant stream power and occur relatively frequently. Out-of-season floods are acknowledged to create more significant changes to river morphology than those that occur during typical wet seasons (Lytle, 2003; Giller, 2005, Wetter et al. 2010).

Concurrent changes

At the onset of a natural flood event, the increasing discharge raises flow velocities, and the thalweg of the river channel deepens and widens (Figure 2). Subsequently mobilization and deposition patterns reverse: pools are scoured and deposition takes place at the riffle areas, with little difference in water depth and velocity between pools and riffles (velocity-reversal phenomenon, Keller and Florsheim, 1993; Thompson et al., 1999, Hogan and Church, 1989). The temperature can either increase (e.g. in consequence of warm thunderstorms) or decrease (e.g. snowmelt waters), but it generally becomes more diverse across a cross-sectional profile (Tockner et al., 2000).

The extent of habitat change is also a function of river type and morphology (e.g., Tockner et al., 2000; Magoulick and Kobza, 2003). In constrained rivers, floods raise flow velocity and shear stress, creating major changes in channel morphology through the scouring and filling of the streambed (Gordon et al., 2004; Vezza et al., 2014). In lowland rivers with extensive floodplains, flood energy is more easily dissipated and water velocity and shear stress may not increase significantly. Nutrients previously deposited on the floodplain are also mobilized, affecting water quality and potentially greatly increasing rates of primary production (Edwards et al., 2012, Davis et al. 2018). Floods fill wetlands, anabranches and flood runners with a slow-moving flow that recedes slowly, and deposits sediments and organic particles upon the floodplain.

Post disturbance effects

Floods reshape the distribution and composition of habitat. The consequences may range from spatial rearrangement of habitats, but 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). In some cases, the morphology of the channel returns to pre-flood conditions (dynamic equilibrium), but this depends on lower flows being sufficiently powerful to move sediments. Thus, recovery is partly determined by river and sediment type.

HABITAT CHANGES CAUSED BY DROUGHTS

Droughts can be divided into those that cause predictable, seasonal press disturbances and less predictable, protracted 'ramp' disturbances (Humphries 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). Droughts tend to be more spatially extensive than floods, which are frequently limited to individual basins (Edwards et al., 2012).

Concurrent changes

During a drought, precipitation, runoff, soil moisture, groundwater levels and stream flow decline sequentially (Changnon, 1987; Grigg, 1996; Dahm et al., 2003). Similar to floods, there are both direct and indirect effects on stream habitat during the drought. Direct effects include loss of habitat area for aquatic organisms and loss of stream connectivity (Lake, 2003, Magoulick & Kobza 2003, Matthews & Marsh-Matthews 2003, Marshall et al. 2016, White et al. 2016).

Loss of habitat is caused by a lack of flow replenishment from upstream and may be exacerbated by evaporation and loss of water into the ground. Indirect effects include deterioration of water quality caused by increased concentration of organic matter that occur despite lower overall input of nutrients (Dewson et al., 2007; Golladay and 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, fine particles and organic matter are deposited on the river bed and into interstitial spaces (McKenzie-Smith et al., 2006). 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., 2003). During hot periods, a continuous increase of water temperature is sometimes accompanied by reduced inflow of cooler groundwater and consequent loss of thermal refugia (Elliot, 2000; Torgersen et al., 1999) and lower oxygen solubility. Higher temperatures increase decomposition rates and thus, further reduce oxygen concentrations. 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 decline during droughts.

Post disturbance effects

Long-term changes depend on drought intensity, duration and the ability of the ecosystem to recover. The changes are mostly of a morphological and/or chemical nature, and among others are consequences of ice-induced scour or sedimentation. Growth of macrophytes and riparian vegetation during droughts can create new morphological patterns after the event (Gurnell 2014, Gurnell et al. 2016a, 2016b). 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 and Mitchell, 2000; Lamontagne et al., 2006).

BIOLOGICAL RESPONSE

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). A third type of response is opportunistic utilization of habitats that are created by the disturbance, such as spawning or feeding habitats (e.g., Grift et al., 2001; Welcomme, 1979, Gorski et al. 2010, 2011, Phelps et al. 2015, Van Looy et al. 2019). Resistance is observed concurrently with disturbance events, while resilience is expressed during the post-disturbance phase. Opportunism can be observed in both phases. Figure 1 represents this concept for the example of floods.

Figure 1 here

Biological responses are triggered by changes in habitat area and quality that fall outside the normal range. Physico-chemical habitat quality attributes are related to flow velocity, water depth, substrate stability, temperature and water quality. These factors affect organisms at the scale at which they perceive their environment (i.e. river element and hydraulic unit; see Gurnell et al 2014). Once the factors exceed the typical suitable range they cause resistance reactions that include: changes in habitude (i.e. organisms occupy sub-optimal habitats when favorable habitats are lost), behavior (e.g. the drag-minimizing body posture and adhesive anchoring observed in some invertebrates (Schnauder et al. 2010) or body size related swimming performance (Wolter & Arlinghaus 2003, Radinger & Wolter 2014)) and a search for areas offering refuge (Lancaster and Belyea, 1997; Meffe, 1984). Resilience is driven by the availability of refugia, connectivity and the organism's fecundity and flexibility of life history strategy (Arlinghaus & Wolter 2003, Klemetsen et al. 2003, Wolter et al. 2016, Van Looy et al. 2019). Opportunism is a function of species being able to take advantage of circumstances during the disturbance.

BIOLOGICAL RESPONSE TO FLOODS

Concurrent response

Floods increase the overall wetted area, although much of this area may be uninhabitable due to high velocities, suspended solids or chemical loads (e.g., Moffett, 1936; Hoopes, 1974). This is followed by change of habitude from, for example, foraging to refuge seeking (Bolland et al. 2015). In rivers without floodplains, the consequence is a reduction of abundance and diversity of macroinvertebrates and juvenile fish (Bischoff & Wolter 2001). Adult fish may also be affected by displacement and injury caused by moving debris and bed instability, or by a shortage of food (Jensen and Johnsen, 1999; Lusk et al., 1998; Weng et al., 2001, Hogberg & Pegg 2015). Extreme events may scour eggs and prevent hatching (Peterson et al. 2000, Carline and McCullough, 2003; Cowx and de Jong, 2004; Phillips et al., 1975, Dusterhoff et al. 2017).

In terms of opportunism, salmonids for example are well adapted to high velocities and use floods to reach spawning grounds that are not accessible or suitable during lower flows (DeVries, 1997). Inundation of the floodplains of low gradient rivers causes a net increase in habitat area for many fish species, and offers refuge and foraging habitat (Schwartz & Herricks 2005, Beesley et al. 2014). The available flooded areas will also determine fish productivity, growth and survival and, accordingly, density of juvenile year classes, especially in spring (Copp 1989, Holčík 1996, Coops et al. 2008, Gorski et al. 2010, 2011, 2013, 2014). The additional influx of nutrients supports rapidly-growing populations of macroinvertebrates (Hickey and Salas, 1995). Allochthonous inputs and high autochthonous floodplain production dominate ecological processes (Humphries et al., 2014, Davis et al. 2018). This creates an abundance of prey for fish (Allen, 1993; Junk et al., 1989). The abundance of phytophilous and phytolithophilous species increases due to higher food and shelter availability (Jurajda et al., 2004, Schomaker & Wolter 2011). However, such a situation is less common during winter floods.

Post-disturbance effects

Overall the most important consequence of flooding is shift of the species composition towards fish species that are better adapted to, or even dependent on, floodplain habitats (Bayley, 1991; Jurajda et al., 2006; Maher, 1994; Leitman et al., 1991, Bischoff & Wolter 2001, Schomaker & Wolter 2011). Due to high mobility of aquatic organisms, the recolonization of highly disturbed areas rapidly takes place, although the rate is strongly dependent on availability and quality of refugia (Magoulick and Kobza, 2003; Townsend, 1989) and species-specific dispersal ability (Radinger & Wolter 2015, Radinger et al. 2017, 2018).

Furthermore, species composition and densities after recovery depend on many morphological changes caused by floods (Elwood and Waters, 1969).

BIOLOGICAL RESPONSE TO DROUGHTS

Concurrent response

Reduction of habitat area during drought conditions is not only due to a smaller wetted area, but also to reduced habitat suitability (e.g. due to excessive temperatures or nutrients). Many fish change their behavior, adjusting to the new conditions (Elliot, 2000, 2006; Davey et al. 2006, Dekar and Magoulick, 2007). For organisms that prefer shallow and low-velocity zones (e.g. invertebrates and juvenile fish), or that are tolerant to high temperature and low oxygen, the amount of suitable habitat may initially increase (Reid et al. 2013). As wetted area further declines, the densities of these organisms increase (Matthews et al. 1994, Dewson et al., 2003; McIntosh et al., 2002). Soon food availability declines and predation increases. The numbers of invertebrates decline and fish assemblage structure changes as a consequence (Arthington et al., 2005; Wood et al., 2000, White et al. 2016).

In perennial streams, the richness of macroinvertebrate species declines due to the loss of habitat diversity. In contrast, the same phenomenon leads to local increases in fish species richness in remnant pools. However, this is an artefact of relocation of fish from dried up areas (Pires et al., 2010). Again, predation by fish and other vertebrates becomes a limiting factor for macroinvertebrates (Labbe and Fausch, 2000; Maceda-Veiga et al., 2009).

Since large portions of aquatic zones become terrestrial, sedentary and sessile species such as freshwater mussels are at risk of stranding, desiccation and predation. The temperature increase in expanding shallow margins also exposes such organisms to thermal shock (Castelli et al., 2012).

Long lasting effects

The overall consequence of drought is a change in species composition towards drought-tolerant, small-bodied species, i.e. those for which habitat conditions have actually improved (e.g. Boix et al, 2010, Schomaker & Wolter 2011, Ruhí et al. 2015, Leigh & Datry 2017). As drought persists and water quality exceeds critical thresholds, the numbers of individuals rapidly declines (Extence, 1981). For fish, the timing of drought is important, as it may affect sensitive life history stages such as spawning or egg incubation. This shapes community composition in future years by potentially causing the failure of entire year classes. Fish and macroinvertebrates can recover quickly from short-term droughts, but the availability of refugia during the drought is critical for this (Covich et al., 2003; Fenoglio et al., 2006; Matthews and Marsh-Matthews, 2003). If cease-to-flow conditions occur, populations may go locally extinct unless aquatic dispersers have made it to permanent water. Populations can be re-established by subsequent high-flow events. Recovery from longer-term droughts that span multiple years is slower because of the smaller pool of surviving organisms. The impacts of supra-seasonal droughts are difficult to predict because of our limited experience of these events (Lake, 2007, Ruhí et al. 2015).

WHAT AFFECTS THE INTENSITY AND DIRECTION OF BIOLOGICAL RESPONSE?

The above sections allow recognition of a general pattern of biological response. Floods and droughts may lead to a change in aquatic community composition, impacting upon the organisms less adapted to the disturbance and promoting those better adapted. During flooding, the mechanisms leading to these changes are drift, injury, dislocation, and concurrent and post-disturbance habitat modifications. However, the flood is not solely a damaging disturbance, but also a major regenerator of biodiversity and production. Drought in contrast leads at coarse scales to net loss of populations through habitat limitation, predation and food shortages. Consequently, a general observation is that predictable floods tend to increase fish species richness, abundance and biomass, whereas droughts lead to a decline (Figure 2).

Figure 2 here

Still, the conceptual model in Figure 2 is generic and some studies have found different results for individual cases (Piniewski et al 2016). One of more significant covariates causing such deviations is the morphological variability of rivers and floodplains. The presence of refugia has a direct effect on survival of animals, and is therefore important for the speed and scale of recolonization. Spatial variability not only mitigates deleterious impacts by providing refugia, but also by offering a diversity of habitats that increase richness, abundance, biomass, recruitment and productivity prior to any disturbance. Habitat shifts also occur for aquatic biota, caused by changes in discharge and resulting changes in flow velocities, shear forces and water levels (e.g. Wolter et al. 2016). For example, in lowland floodplain rivers, the occurrence of hydraulically inhospitable habitats (i.e. very fast flowing) is compensated for by the creation of vast areas of attractive spawning and larval rearing habitats on the floodplain (Gorski et al. 2010, 2011, van de Wolfshaar et al. 2011, Stoffels et al. 2015). In high-gradient rivers, floods create access to tributaries, effectively expanding accessible habitat area (e.g. Sukhodolov et al. 2009).

The intensity of biological response also depends upon factors such as geographic location and seasonality. For example, a drought of the same magnitude will have different consequences in northern and southern Europe. In some Mediterranean streams, adaptation to climatic regimes means that fish can survive much more severe droughts that would be lethal to any northern organisms (Horne et al., in review).

Similar differences in response are seen with the timing of disturbance. For example, in many rivers of the northern hemisphere severe flooding in summer has different biological consequences than during the spring (spawning) time. Since summers are characterized by low-flow conditions, many animals utilize habitat for rearing and growth, with extensive nursery habitats (Olaya-Marin et al., 2013). Unpredictable floods (e.g. unseasonal or happening with higher frequency than in the past) have been documented as having very deleterious effects on fish assemblages (Bischoff & Wolter 2001,George et al. 2015, Hogberg & Pegg 2015).

Consequently, the intensity of biological responses to disturbance events depends on their predictability; populations become adapted to the conditions that are most common, and the frequency of occurrence in the past is a driver of the predictability.

PREDICTING IMPACT OF CLIMATE CHANGE ON ECOLOGICALLY-RELEVANT FLOW REGIMES

A recent work projecting hydrologic response to future weather data derived from various IPCC global circulation models for the state of New Hampshire, USA provides some insight on how the climate change could modify hydrologic patterns (Bjerklie and Sturtevant, 2017). This state wide analysis documented a common pattern characterised by an increase of higher flows over cold season and lower flows during spring and summer. The study also projected increased variability of flows, with changes to the magnitude of baseflows (groundwater inflow) varying depending on elevation and micro-climatic factors related to location. The variability of the flow response to climate changes within the state is demonstrated by comparing flow duration curves of a relatively small coastal river the Oyster River and the larger Pemigewassett River (Bjerklie et al., 2015). Although both of them follow the described trend it is more pronounced in the Pemigewassett River. The Oyster River has little topographic relief and sandy soils, while the Pemigewassett River is located in the upland and more mountainous terrain (Bjerklie et al., 2015).

The question about the way in which predicted river flow changes will mediate climate change signal on biota is rather complex due to many confounding factors. The majority of the model-based climate change impact studies deal with ‘ecologically relevant’ flow regimes (Dhungel et al. 2016, Döll & Zhang 2010, Laizé et al. 2013, Morales-Marin et al. 2019, O'Keeffe et al. 2018, Piniewski et al. 2014, Stagl and Hattermann 2016, Van Vliet et al. 2013, Vigiak et al. 2018) whereby ‘ecological relevance’ is usually assessed based on available literature. This approach is better suited for large-scale analyses: from global (Döll &

Zhang), through continental (Laizé et al. 2013, Van Vliet et al. 2013) to national (Dhungel et al. 2016) and large river basin scale (O'Keeffe et al. 2018, Stagl and Hattermann 2016). Predicted effects of climate change on riverine biota are only implicit in such studies. For example, O'Keeffe et al. (2018) reported a projected increase in high flow frequency in the Vistula and Odra basins in Poland, which could be beneficial for northern pike due to more frequent floodplain inundation and better river-floodplain connectivity. On the other hand, abnormally high streamflow could wash away the fish and eggs.

In a more complex approach, but typically applied at finer spatial scales, climate change forcing is propagated through a modelling cascade consisting of a hydrological model loosely coupled with a habitat suitability or a species distribution model (Jaeger et al. 2014, Kakouei et al. 2018, Kuemmerlen et al. 2015, Morid et al. 2016, Muñoz-Mas et al. 2016, Mustonen et al. 2018, Viganò et al. 2015, Woznicki et al. 2016). For example, Jaeger et al. (2014) predicted a higher frequency of zero-flow days in an intermittent stream in Arizona, United States, which would inevitably lead to more channel fragmentation and a reduced network-wide hydrological connectivity during spawning of native fish.

Yet higher level of complexity can be achieved by including a hydraulic model in the modelling chain, yet such approaches are typically applied only at small catchment scales (Guse et al. 2015, Papadaki et al. 2016). Papadaki et al (2016) showed that the West Balkan trout is likely to expect a deterioration in habitat quantity and quality in summer months in a mountainous stream in Greece. In contrast, Guse et al. (2015) reported variable changes in habitat suitability for fishes in a small stream in northern Germany in response to climate change. They also predicted a dampened effect of climate change on stream hydraulics compared to the effects on discharge itself.

DISCUSSION

Our review underlines the importance of floods and droughts as a master driving force of the riverine ecosystems that shape the biotic communities. Each of these events creates immediate and long lasting modification of habitat conditions for riverine flora and fauna.

This in turn causes specific biological response that leads to change of composition of aquatic communities, also in short and long term.

The response may be in form of resistance, change of habitude and resilience. The intensity and direction of biological impact may vary depending on location and particular climatic and physiographic setting of the watershed. The variety of impact will further diversify if we include other human-induced alterations to riverine ecosystems. For example, a good demonstration of the consequences of dam construction is presented in a study on the Tana River in Kenya (Langat et al 2019).

Nevertheless, the expected overall long term consequence of natural floods and droughts regime is an increase in biological diversity and ecosystem health. Hence, floods and droughts can be seen as “rejuvenating” events essential for ecological equilibrium. Therefore, sudden and dramatic alteration of floods and droughts pattern as expected in climate change perspective may cause dramatic changes in the structure and composition of aquatic communities. Quantification of these changes is therefore key to prediction of biological consequences of climate change. To capture these modifications descriptive pattern metrics, which are directly related to biological response need to be identified.

As presented by Humphries et al. (2014) in the River Wave Concept, river flow may be conceptualized as series of waves varying in shape, amplitude, wavelength, and frequency. Floods are crests and droughts are the troughs of the wave and define its overall characteristics. These attributes can be used as hydrologic metrics to characterize the pattern of disturbance events.

As presented above the aquatic organisms evolved around the hydrologic events that are predictable and therefore more common. Hence, the event frequency is a wave metric most closely related to disturbance predictability and consequently intensity of biological response. It is in a reverse relationship i.e. the higher the natural frequency, the higher the probability the less intense the biological alteration (Figure 3).

The relationship between the metrics of event intensity and frequency is generally described by a power law (Bak, 1996). In undisturbed ecosystems the disturbances of large magnitude or duration are much less frequent and vice versa. Consequently, events of extreme magnitude and/or duration (floods or droughts) can be expected to have a much stronger biological effect, in that they may even cause a depletion or expansion of populations. The smallest and most frequent events commonly cause a change of habitude, as the migration to refuge sets on (Figure 3).

Figure 3 here

According to Lake (2000), floods are pulse disturbances and the response to floods is most often of a pulse type. However, extreme floods that create dramatic hydromorphologic change will cause a press response. In both cases, flood magnitude is a stronger driver than event duration.

Since floods are generally pulse disturbances, the key attributes related to biological response are flood **frequency** and **magnitude**. Consequently, there is a functional relationship between these two metrics and the intensity of biological impact of floods. In regions where the hydrologic response to climate change is towards increasing frequency of high flow events, resulting in significant change to the flow regime, the channel will try to widen and deepen its cross-section to accommodate the more frequent flooding. The time frame for the river to adjust to a more stable geometry is intricately associated with the time for instream habitat to adjust. If the response also includes larger flood events, adjustments to the channel morphology may also include changes to the planform structure of the river network, including changes to the meandering pattern and associated riverine floodplain features such as wetlands and ponds. Additionally, changes in flood frequency and magnitude will markedly change the amount of woody debris entering the river channel, and the amount of sediment transported to downstream areas. Subsequently, the relative alteration of flood magnitude and frequency that is caused by climate change is intricately tied to, and can be indicative of, biological response to climate change.

Since droughts are presses and ramps, the response is also a ramp. Here, the key driver of biological response is **drought duration** (Figure 4). In addition, increased **frequency** even of small disturbance events can also be a cause of ramp responses. For example, increased frequency of smaller drought events that happen during supra-seasonal droughts will further affect the physical condition of fauna and may lead to catastrophic consequences.

Figure 4 here

ACKNOWLEDGMENTS:

Special thanks go Marta Gonzales del Tanago, Diego Garcia de Jalon of Madrid Politechnic and Tomasz Okruszko of Polish University of Life Sciences for their valuable comments and support for this work. Much of this work was conducted with Funding Support from European Commission within REFORM project (GA 282656). Data collection for the case study was funded by Polish National Water Authority within Environmental Flow Method Determination Study.

REFERENCES

Allen, W. H. (1993). The great flood of 1993. BioScience, 43(11), 732-737.

Arlinghaus, R., & Wolter, C. (2003). Amplitude of ecological potential: chub Leuciscus cephalus (L.) spawning in an artificial lowland canal. *Journal of Applied Ichthyology*, *19*(1), 52-54.

Arnold, J. G., Srinivasan, R., Muttiah, R. S., & Williams, J. R. (1998). Large area hydrologic modeling and assessment part I: model development 1. *JAWRA Journal of the American Water Resources Association*, *34*(1), 73-89.

Arthington, A. H., Balcombe, S. R., Wilson, G. A., Thoms, M. C., & Marshall, J. (2005). Spatial and temporal variation in fish-assemblage structure in isolated waterholes during the 2001 dry season of an arid-zone floodplain river, Cooper Creek, Australia. *Marine and Freshwater Research*, *56*(1), 25-35.

Bak P. 1996. How Nature Works. Copernicus: New York, NY; 212.

Baldwin, D. S., & Mitchell, A. M. (2000). The effects of drying and re‐flooding on the sediment and soil nutrient dynamics of lowland river–floodplain systems: a synthesis. *Regulated rivers: research & management*, *16*(5), 457-467.

Bayley, P. B. (1991). The flood pulse advantage and the restoration of river‐floodplain systems. *Regulated Rivers: Research & Management*, *6*(2), 75-86.

Beesley, L. S., Gwinn, D. C., Price, A., King, A. J., Gawne, B., Koehn, J. D., & Nielsen, D. L. (2014). Juvenile fish response to wetland inundation: how antecedent conditions can inform environmental flow policies for native fish. *Journal of Applied Ecology*, *51*(6), 1613-1621.

Bischoff, A., & Wolter, C. (2001). The flood of the century on the River Oder: effects on the 0+ fish community and implications for floodplain restoration. *Regulated Rivers: Research & Management: An International Journal Devoted to River Research and Management*, *17*(2), 171-190.

Blöschl, G., Hall, J., Parajka, J., Perdigão, R. A., Merz, B., Arheimer, B., ... & Čanjevac, I. (2017). Changing climate shifts timing of European floods. *Science*, *357*(6351), 588-590.

Boix, D., García-Berthou, E., Gascón, S., Benejam, L., Tornés, E., Sala, J., ... & Sabater, S. (2010). Response of community structure to sustained drought in Mediterranean rivers. *Journal of Hydrology*, *383*(1-2), 135-146.

Bolland, J. D., Nunn, A. D., Lucas, M. C., & Cowx, I. G. (2015). The habitat use of young-of-the-year fishes during and after floods of varying timing and magnitude in a constrained lowland river. *Ecological Engineering*, *75*, 434-440.

Bork, HR, & Kranz, A. (2008). The millennium flood of the year 1342 characterizes Germany-New research results from the catchment area of the Main. *Annual Report of the Wetterau Society for Natural History* , *158* , 119-129.

Bormann, H., & Pinter, N. (2017). Trends in low flows of German rivers since 1950: Comparability of different low‐flow indicators and their spatial patterns. *River Research and Applications*, *33*(7), 1191-1204.

Carline, R. F., & McCullough, B. J. (2003). Effects of floods on brook trout populations in the Monongahela National Forest, West Virginia. *Transactions of the American Fisheries Society*, *132*(5), 1014-1020.

Castelli, E., Parasiewicz, P., & Rogers, J. N. (2011). Use of frequency and duration analysis for the determination of thermal habitat thresholds: application for the conservation of Alasmidonta heterodon in the Delaware River. *Journal of Environmental Engineering*, *138*(8), 886-892.

Changnon, S. A. (1987). Detecting drought conditions in Illinois. *Circular no. 169*.

Coops, H., Buijse, L. L., Buijse, A. D., Constantinescu, A., Covaliov, S., Hanganu, J., ... & Staras, M. (2008). Trophic gradients in a large-river Delta: ecological structure determined by connectivity gradients in the Danube Delta (Romania). *River Research and Applications*, *24*(5), 698-709.

Copp, G. H. (1989). The habitat diversity and fish reproductive function of floodplain ecosystems. Environmental Biology of Fishes, 26(1), 1-27. doi:10.1007/bf00002472.

Costa, J. E., & O'Connor, J. E. (1995). Geomorphically effective floods. *Natural and anthropogenic influences in fluvial geomorphology*, *89*, 45-56.

Covich, A. P., Crowl, T. A., & Scatena, F. N. (2003). Effects of extreme low flows on freshwater shrimps in a perennial tropical stream. *Freshwater Biology*, *48*(7), 1199-1206.

Cowx IG, de Jong MV. 2004. Rehabilitation of freshwater fisheries: tales of the unexpected? *Fisheries Management and Ecology* **11**: 243-249.

Dahm, C. N., Baker, M. A., Moore, D. I., & Thibault, J. R. (2003). Coupled biogeochemical and hydrological responses of streams and rivers to drought. *Freshwater biology*, *48*(7), 1219-1231.

Davey, A. J. H., Kelly, D. J., & Biggs, B. J. F. (2006). Refuge-use strategies of stream fishes in response to extreme low flows. *Journal of Fish Biology*, *69*(4), 1047-1059.

Davis, A. M., Pusey, B. J., & Pearson, R. G. (2018). Big floods, big knowledge gap: Food web dynamics in a variable river system. *Ecology of Freshwater Fish*, *27*(4), 898-909.

Death, R. G., Fuller, I. C., & Macklin, M. G. (2015). Resetting the river template: the potential for climate-related extreme floods to transform river geomorphology and ecology. *Freshwater Biology*, *60*(12), 2477-2496.

Dekar, M. P., & Magoulick, D. D. (2007). Factors affecting fish assemblage structure during seasonal stream drying. *Ecology of Freshwater Fish*, *16*(3), 335-342.

DeVries, P. (1997). Riverine salmonid egg burial depths: review of published data and implications for scour studies. *Canadian Journal of Fisheries and Aquatic Sciences*, *54*(8), 1685-1698.

Dewson, Z. S., James, A. B., & Death, R. G. (2007). A review of the consequences of decreased flow for instream habitat and macroinvertebrates. *Journal of the North American Benthological Society*, *26*(3), 401-415.

Dotterweich, M. (2008). The history of soil erosion and fluvial deposits in small catchments of central Europe: deciphering the long-term interaction between humans and the environment—a review. *Geomorphology*, *101*(1-2), 192-208.

Dusterhoff, S. R., Sloat, M. R., & Ligon, F. K. (2017). The influence of coarse particle mobility on scour depth in salmonid spawning habitat. River Research and Applications, 33(8), 1306-1314. doi:10.1002/rra.3178.

Edwards FK, Baker R, Dunbar M, Laize C. 2012. Deliverable 2.14: Review on processes and effects of droughts and summer floods in rivers and threats due to climate change on current adaptive management strategies. EU FP7 REFRESH deliverable 2.14. pp75. Published online: http://www.refresh.ucl.ac.uk/webfm_send/1860http://www.refresh.ucl.ac.uk/webfm_send/1860.

Eisner, S., Flörke, M., Chamorro, A., Daggupati, P., Donnelly, C., Huang, J., ... & Mishra, V. (2017). An ensemble analysis of climate change impacts on streamflow seasonality across 11 large river basins. *Climatic change*, *141*(3), 401-417.

Elliott, J. M. (2000). Pools as refugia for brown trout during two summer droughts: trout responses to thermal and oxygen stress. *Journal of fish biology*, *56*(4), 938-948.

Elliott, J. M. (2006). Periodic habitat loss alters the competitive coexistence between brown trout and bullheads in a small stream over 34 years. *Journal of Animal Ecology*, *75*(1), 54-63.

Elwood, J. W., & Waters, T. F. (1969). Effects of floods on food consumption and production rates of a stream brook trout population. *Transactions of the American Fisheries Society*, *98*(2), 253-262.

Extence, C. A. (1981). The effect of drought on benthic invertebrate communities in a lowland river. *Hydrobiologia*, *83*(2), 217-224.

Fenoglio, S., Bo, T., & Bosi, G. (2006). Deep interstitial habitat as a refuge for Agabus paludosus (Fabricius)(Coleoptera: Dytiscidae) during summer droughts. *The Coleopterists Bulletin*, *60*(1), 37-42.

Fisher, S. G., Gray, L. J., Grimm, N. B., & Busch, D. E. (1982). Temporal succession in a desert stream ecosystem following flash flooding. *Ecological monographs*, *52*(1), 93-110.

Fisher, S. G., & Grimm, N. B. (1991). Streams and disturbance: Are cross-ecosystem comparisons useful?. In *Comparative Analyses of Ecosystems* (pp. 196-221). Springer, New York, NY.

Frissell, C. A., Liss, W. J., Warren, C. E., & Hurley, M. D. (1986). A hierarchical framework for stream habitat classification: viewing streams in a watershed context. *Environmental management*, *10*(2), 199-214.

Fuller, I. C., Gilvear, D. J., Thoms, M. C., & Death, R. G. (2019). Framing resilience for river geomorphology: Reinventing the wheel?. *River Research and Applications*, *35*(2), 91-106.

Garner, G., Van Loon, A. F., Prudhomme, C., & Hannah, D. M. (2015). Hydroclimatology of extreme river flows. *Freshwater biology*, *60*(12), 2461-2476.

George, S. D., Baldigo, B. P., Smith, A. J., & Robinson, G. R. (2015). Effects of extreme floods on trout populations and fish communities in a C atskill M ountain river. *Freshwater Biology*, *60*(12), 2511-2522.

Giller, P. S. (2005). River restoration: seeking ecological standards. Editor's introduction. *Journal of Applied Ecology*, *42*(2), 201-207.

Glaser, R., Riemann, D., Schönbein, J., Barriendos, M., Brázdil, R., Bertolin, C., ... & Enzi, S. (2010). The variability of European floods since AD 1500. *Climatic Change*, *101*(1-2), 235-256.

Golladay, S. W., & Battle, J. (2002). Effects of flooding and drought on water quality in gulf coastal plain streams in Georgia. *Journal of Environmental Quality*, *31*(4), 1266-1272.

Gordon, N. D., McMahon, T. A., Finlayson, B. L., & Gippel, C. J. (2004). *Stream hydrology: an introduction for ecologists*. John Wiley and Sons.

Górski, K., Buijse, A. D., Winter, H. V., De Leeuw, J. J., Compton, T. J., Vekhov, D. A., ... & Nagelkerke, L. A. J. (2013). Geomorphology and flooding shape fish distribution in a large-scale temperate floodplain. *River Research and Applications*, *29*(10), 1226-1236.

Górski, K., Collier, K. J., Hamilton, D. P., & Hicks, B. J. (2014). Effects of flow on lateral interactions of fish and shrimps with off-channel habitats in a large river-floodplain system. *Hydrobiologia*, *729*(1), 161-174.

Gorski, K., De Leeuw, J. J., Winter, H. V., Vekhov, D. A., Minin, A. E., Buijse, A. D., & Nagelkerke, L. A. (2011). Fish recruitment in a large, temperate floodplain: the importance of annual flooding, temperature and habitat complexity. *Freshwater Biology*, *56*(11), 2210-2225.

Górski, K., Winter, H. V., De Leeuw, J. J., Minin, A. E., & Nagelkerke, L. A. J. (2010). Fish spawning in a large temperate floodplain: the role of flooding and temperature. *Freshwater Biology*, *55*(7), 1509-1519.

Grift, R. E., Buljse, A. D., Breteler, J. K., Densen, W. V., Machiels, M. A. M., & Backx, J. J. M. (2001). Migration of bream between the main channel and floodplain lakes along the lower River Rhine during the connection phase. *Journal of Fish Biology*, *59*(4), 1033-1055.

Grigg, N. S. (1996). *Water resources management: principles, regulations, and cases* (No. 631.7 G72). New York: McGraw-Hill.

Grossman, G. D., Moyle, P. B., & Whitaker Jr, J. O. (1982). Stochasticity in structural and functional characteristics of an Indiana stream fish assemblage: a test of community theory. *The American Naturalist*, *120*(4), 423-454.

Grossman, G. D., Moyle, P. B., & Whitaker Jr, J. O. (1982). Stochasticity in structural and functional characteristics of an Indiana stream fish assemblage: a test of community theory. *The American Naturalist*, *120*(4), 423-454.

Gurnell, A. M., Belletti, B., Bizzi, S., Blamauer, B., Braca, G., Buijse, A. D., ... & García De Jalón, D. (2014). A hierarchical multi-scale framework and indicators of hydromorphological processes and forms. *Project Report REFORM D*, *2*.

Gurnell, A. (2014). Plants as river system engineers. *Earth Surface Processes and Landforms*, *39*(1), 4-25.

Gurnell, A. M., Corenblit, D., García de Jalón, D., González del Tánago, M., Grabowski, R. C., O'hare, M. T., & Szewczyk, M. (2016). A conceptual model of vegetation–

hydrogeomorphology interactions within river corridors. *River research and applications*, *32*(2), 142-163.

Gurnell, A. M., Rinaldi, M., Belletti, B., Bizzi, S., Blamauer, B., Braca, G., ... & Demarchi, L. (2016). A multi-scale hierarchical framework for developing understanding of river behaviour to support river management. *Aquatic Sciences*, *78*(1), 1-16.

Guse, B., Kail, J., Radinger, J., Schröder, M., Kiesel, J., Hering, D., ... & Fohrer, N. (2015). Eco-hydrologic model cascades: Simulating land use and climate change impacts on hydrology, hydraulics and habitats for fish and macroinvertebrates. *Science of the Total Environment*, *533*, 542-556.

Hauer, C., & Habersack, H. (2009). Morphodynamics of a 1000-year flood in the Kamp River, Austria, and impacts on floodplain morphology. *Earth Surface Processes and Landforms*, *34*(5), 654-682.

Herget, J., Kapala, A., Krell, M., Rustemeier, E., Simmer, C., & Wyss, A. (2015). The millennium flood of July 1342 revisited. *Catena*, *130*, 82-94.

Hickey JT, Salas JD. 1995. Environmental effects of extreeme floods. Proceedings of U.S.-Italy Research Workshop on the Hydrometeorology, Impacts, and Management of Extreme Floods Perugia (Italy), November 1995.

Hogan, D. L., & Church, M. (1989). Hydraulic geometry in small, coastal streams: progress toward quantification of salmonid habitat. *Canadian Journal of Fisheries and Aquatic Sciences*, *46*(5), 844-852.

Hogberg, N. P., & Pegg, M. A. (2016). Assessment of fish floodplain use during an extreme flood event in a large, regulated river. *Hydrobiologia*, *765*(1), 27-41.

Holčík, J. (1996). Ecological fish production in the inland delta of the Middle Danube, a floodplain river. *Environmental biology of fishes*, *46*(2), 151-165.

Hoopes, R. L. (1974). Flooding, as the result of Hurricane Agnes, and its effect on a macrobenthic community in an infertile headwater stream in central Pennsylvania. *Limnology and oceanography*, *19*(5), 853-857.

Horne AC, Nathan R, Poff NL, Bond NR, Webb JA . Modelling flow-ecology responses in the Anthropocene: challenges for sustainable riverine management. *Bioscience*.

Humphries, P., Keckeis, H., & Finlayson, B. (2014). The river wave concept: integrating river ecosystem models. *BioScience*, *64*(10), 870-882.

Jensen, A. J., & Johnsen, B. O. (1999). The functional relationship between peak spring floods and survival and growth of juvenile Atlantic salmon (Salmo salar) and brown trout (Salmo trutta). *Functional Ecology*, *13*(6), 778-785.

Junk, W. J. (2005). Flood pulsing and the linkages between terrestrial, aquatic, and wetland systems. *Internationale Vereinigung für theoretische und angewandte Limnologie: Verhandlungen*, *29*(1), 11-38.

Jurajda, P., Ondračková, M., & Reichard, M. (2004). Managed flooding as a tool for supporting natural fish reproduction in man-made lentic water bodies. *Fisheries Management and Ecology*, *11*(3-4), 237-242.

Jurajda, P., Reichard, M., & Smith, C. (2006). Immediate impact of an extensive summer flood on the adult fish assemblage of a channelized lowland river. *Journal of Freshwater Ecology*, *21*(3), 493-501.

Keller, E. A., & Florsheim, J. L. (1993). Velocity-reversal hypothesis: A model approach. *Earth Surface Processes and Landforms*, *18*(8), 733-740.

Klemetsen, A., Amundsen, P. A., Dempson, J. B., Jonsson, B., Jonsson, N., O'connell, M. F., & Mortensen, E. (2003). Atlantic salmon Salmo salar L., brown trout Salmo trutta L. and Arctic charr Salvelinus alpinus (L.): a review of aspects of their life histories. *Ecology of freshwater fish*, *12*(1), 1-59.

Labbe, T. R., & Fausch, K. D. (2000). Dynamics of intermittent stream habitat regulate persistence of a threatened fish at multiple scales. *Ecological Applications*, *10*(6), 1774-1791.

Lake, P. S. (2000). Disturbance, patchiness, and diversity in streams. *Journal of the north american Benthological society*, *19*(4), 573-592.

Lake, P. S. (2003). Ecological effects of perturbation by drought in flowing waters. *Freshwater biology*, *48*(7), 1161-1172.

Lake, P. S. (2008). Flow-generated disturbances and ecological responses: floods and droughts. *Hydroecology and ecohydrology: past, present and future. Wiley Press, New York*, 75-92.

Lake, P. S. (2011). *Drought and aquatic ecosystems: effects and responses*. John Wiley & Sons.

Lamontagne, S., Hicks, W. S., Fitzpatrick, R. W., & Rogers, S. (2006). Sulfidic materials in dryland river wetlands. *Marine and Freshwater Research*, *57*(8), 775-788.

Lancaster, J., & Belyea, L. R. (1997). Nested hierarchies and scale-dependence of mechanisms of flow refugium use. *Journal of the North American Benthological Society*, *16*(1), 221-238.

Langat, P. K., Kumar, L., Koech, R., & Ghosh, M. K. (2019). Hydro-Morphological Characteristics Using Flow Duration Curve, Historical Data and Remote Sensing: Effects of Land Use and Climate. *Water*, *11*(2), 309.

Leigh, C., & Datry, T. (2017). Drying as a primary hydrological determinant of biodiversity in river systems: A broad-scale analysis. *Ecography*, *40*(4), 487-499.

Leitman, H. M., Darst, M. R., & Nordhaus, J. J. (1991). Fishes in the forested flood plain of the Ochlockonee River, Florida, during flood and drought conditions. *Water Resources Investigations Report*, 90-4202.

Lusk, S., Halacˇka, K., & Lusková, V. (1998). The effect of an extreme flood on the fish communities in the upper reaches of the Tichá Orlice River (the Labe drainage area). *Czech Journal of Animal Science*, *43*, 531-536.

Lytle, D. A. (2003). Reconstructing long-term flood regimes with rainfall data: effects of flood timing on caddisfly populations. *The Southwestern Naturalist*, *48*(1), 36-43.

Lytle, D. A., & Poff, N. L. (2004). Adaptation to natural flow regimes. *Trends in ecology & evolution*, *19*(2), 94-100.

Maceda-Veiga, A., Salvadó, H., Vinyoles, D., & De Sostoa, A. (2009). Outbreaks of Ichthyophthirius multifiliis in Redtail Barbs Barbus haasi in a Mediterranean stream during drought. *Journal of Aquatic Animal Health*, *21*(3), 189-194.

Magoulick, D. D., & Kobza, R. M. (2003). The role of refugia for fishes during drought: a review and synthesis. *Freshwater biology*, *48*(7), 1186-1198.

Magoulick, D. D., & Kobza, R. M. (2003). The role of refugia for fishes during drought: a review and synthesis. *Freshwater biology*, *48*(7), 1186-1198.

Matthews, W. J., Harvey, B. C., & Power, M. E. (1994). Spatial and temporal patterns in the fish assemblages of individual pools in a midwestern stream (USA). *Environmental Biology of Fishes*, *39*(4), 381-397.

Maher, R. J. (1993). Observations of fish community structure and reproductive success in flooded terrestrial areas during an extreme flood on the lower Illinois River. *Long term resource monitoring program*, 95-115.

Markovic, D., Carrizo, S. F., Kärcher, O., Walz, A., & David, J. N. (2017). Vulnerability of European freshwater catchments to climate change. *Global change biology*, *23*(9), 3567-3580.

Markovic, D., Scharfenberger, U., Schmutz, S., Pletterbauer, F., & Wolter, C. (2013). Variability and alterations of water temperatures across the Elbe and Danube River Basins. *Climatic Change*, *119*(2), 375-389.

Marshall, J. C., Menke, N., Crook, D. A., Lobegeiger, J. S., Balcombe, S. R., Huey, J. A., ... & Linke, S. (2016). Go with the flow: the movement behaviour of fish from isolated waterhole refugia during connecting flow events in an intermittent dryland river. *Freshwater Biology*, *61*(8), 1242-1258.

Matthews, W. J., & Marsh-Matthews, E. (2003). Effects of drought on fish across axes of space, time and ecological complexity. *Freshwater biology*, *48*(7), 1232-1253.

McIntosh, M. D., Benbow, M. E., & Burky, A. J. (2002). Effects of stream diversion on riffle macroinvertebrate communities in a Maui, Hawaii, stream. *River Research and Applications*, *18*(6), 569-581.

McKee, T. B., Doesken, N. J., & Kleist, J. (1993, January). The relationship of drought frequency and duration to time scales. In *Proceedings of the 8th Conference on Applied Climatology*(Vol. 17, No. 22, pp. 179-183). Boston, MA: American Meteorological Society.

McKenzie-Smith, F. J., Bunn, S. E., & House, A. P. (2006). Habitat dynamics in the bed sediments of an intermittent upland stream. *Aquatic sciences*, *68*(1), 86-99.

McMaster, D., & Bond, N. (2008). A field and experimental study on the tolerances of fish to Eucalyptus camaldulensis leachate and low dissolved oxygen concentrations. *Marine and Freshwater Research*, *59*(2), 177-185.

Meffe, G. K. (1984). Effects of abiotic disturbance on coexistence of predator-prey fish species. *Ecology*, *65*(5), 1525-1534.

Mezghani, A., Dobler, A., Haugen, J. E., Benestad, R. E., Parding, K. M., Piniewski, M., ... & Kundzewicz, Z. W. (2017). CHASE-PL Climate Projection dataset over Poland-bias adjustment of EURO-CORDEX simulations. *Earth Syst. Sci. Data*, *9*, 905-925.

Moffett, J. W. (1935). *A quantitative study of the bottom fauna in some Utah streams variously affected by erosion* (Master's thesis, Dept. of Zoology, University of Utah).

Molles Jr, M. C. (1985). Recovery of a stream invertebrate community from flash a flash flood in Tesuque Creek, New Mexico. *The Southwestern Naturalist*, 279-287.

Myers, B. J., Lynch, A. J., Bunnell, D. B., Chu, C., Falke, J. A., Kovach, R. P., ... & Paukert, C. P. (2017). Global synthesis of the documented and projected effects of climate change on inland fishes. *Reviews in fish biology and fisheries*, *27*(2), 339-361.

O'Connor, W. G., & Koehn, J. D. (1998). Spawning of the broad‐finned Galaxias, Galaxias brevipinnis Günther (Pisces: Galaxiidae) in coastal streams of southeastern Australia. *Ecology of Freshwater Fish*, *7*(2), 95-100.

O'Keeffe, J., Piniewski, M., Szcześniak, M., Oglęcki, P., Parasiewicz, P., & Okruszko, T. (2018). Index-based analysis of climate change impact on streamflow conditions important for Northern Pike, Chub and Atlantic salmon. *Fisheries Management and Ecology*.

Olaya-Marín, E. J., Martínez-Capel, F., & Vezza, P. (2013). A comparison of artificial neural networks and random forests to predict native fish species richness in Mediterranean rivers. *Knowledge and Management of Aquatic Ecosystems*, (409), 07.

Ozga-Zielinska, M. (1989). Droughts and floods-their definition and modeling. *New Directions for Surface Water Modelling*, 313-322.

Parasiewicz, P. (2008). Habitat time series analysis to define flow augmentation strategy for the Quinebaug River, Connecticut and Massachusetts, USA. *River research and applications*, *24*(4), 439-452.

Parasiewicz, P., Prus, P., Suska, K., & Marcinkowski, P. (2018). “E= mc2” of Environmental Flows: A Conceptual Framework for Establishing a Fish-Biological Foundation for a Regionally Applicable Environmental Low-Flow Formula. *Water*, *10*(11), 1501.

Parasiewicz, P., Rogers, J. N., Vezza, P., Gortázar, J., Seager, T., Pegg, M., ... & Comoglio, C. (2013). Applications of the MesoHABSIM simulation model. *Ecohydraulics: An integrated approach*, 109-124.

Parasiewicz, P., Ryan, K., Vezza, P., Comoglio, C., Ballestero, T., & Rogers, J. N. (2013). Use of quantitative habitat models for establishing performance metrics in river restoration planning. *Ecohydrology*, *6*(4), 668-678.

Pearsons, T. N., Li, H. W., & Lamberti, G. A. (1992). Influence of habitat complexity on resistance to flooding and resilience of stream fish assemblages. *Transactions of the American Fisheries society*, *121*(4), 427-436.

Schuett-Hames, D. E., Peterson, N. P., Conrad, R., & Quinn, T. P. (2000). Patterns of gravel scour and fill after spawning by chum salmon in a western Washington stream. *North American Journal of Fisheries Management*, *20*(3), 610-617.

Phelps, Q. E., Tripp, S. J., Herzog, D. P., & Garvey, J. E. (2015). Temporary connectivity: the relative benefits of large river floodplain inundation in the lower Mississippi River. *Restoration Ecology*, *23*(1), 53-56.

Phillips, R. W., Lantz, R. L., Claire, E. W., & Moring, J. R. (1975). Some effects of gravel mixtures on emergence of coho salmon and steelhead trout fry. *Transactions of the American Fisheries Society*, *104*(3), 461-466.

Piniewski, M., Prudhomme, C., Acreman, M. C., Tylec, L., Oglęcki, P., & Okruszko, T. (2017). Responses of fish and invertebrates to floods and droughts in Europe. *Ecohydrology*, *10*(1), e1793.

Piniewski, M., Szcześniak, M., & Kardel, I. (2017). CHASE-PL—Future Hydrology Data Set: Projections of Water Balance and Streamflow for the Vistula and Odra Basins, Poland. *Data*, *2*(2), 14.

Piniewski, M., Szcześniak, M., Kardel, I., Berezowski, T., Okruszko, T., Srinivasan, R., ... & Kundzewicz, Z. W. (2017). Hydrological modelling of the Vistula and Odra river basins using SWAT. *Hydrological Sciences Journal*, *62*(8), 1266-1289.

Piniewski, M., Szcześniak, M., Kundzewicz, Z. W., Mezghani, A., & Hov, Ø. (2017). Changes in low and high flows in the Vistula and the Odra basins: Model projections in the European-scale context. *Hydrological processes*, *31*(12), 2210-2225.

Pires, D. F., Pires, A. M., Collares-Pereira, M. J., & Magalhães, M. F. (2010). Variation in fish assemblages across dry-season pools in a Mediterranean stream: effects of pool morphology, physicochemical factors and spatial context. *Ecology of Freshwater Fish*, *19*(1), 74-86.

Poff, N. L. (1992). Why disturbances can be predictable: a perspective on the definition of disturbance in streams. *Journal of the North American Benthological Society*, *11*(1), 86-92.

Poff, N. L. (2018). Beyond the natural flow regime? Broadening the hydro-ecological foundation to meet environmental flows challenges in a non-stationary world. *Freshwater biology*, *63*(8), 1011-1021.

Poff, N. L., Olden, J. D., Merritt, D. M., & Pepin, D. M. (2007). Homogenization of regional river dynamics by dams and global biodiversity implications. *Proceedings of the National Academy of Sciences*, *104*(14), 5732-5737.

Puckridge, J. T., Sheldon, F., Walker, K. F., & Boulton, A. J. (1998). Flow variability and the ecology of large rivers. *Marine and freshwater research*, *49*(1), 55-72.

Radinger, J., & Wolter, C. (2014). Patterns and predictors of fish dispersal in rivers. *Fish and fisheries*, *15*(3), 456-473.

Radinger, J., & Wolter, C. (2015). Disentangling the effects of habitat suitability, dispersal, and fragmentation on the distribution of river fishes. *Ecological applications*, *25*(4), 914-927.

Radinger, J., Essl, F., Hölker, F., Horký, P., Slavík, O., & Wolter, C. (2017). The future distribution of river fish: The complex interplay of climate and land use changes, species dispersal and movement barriers. *Global change biology*, *23*(11), 4970-4986.

Radinger, J., Hölker, F., Horký, P., Slavík, O., & Wolter, C. (2018). Improved river continuity facilitates fishes' abilities to track future environmental changes. *Journal of environmental management*, *208*, 169-179.

Reice, S. R. (1985). Experimental disturbance and the maintenance of species diversity in a stream community. *Oecologia*, *67*(1), 90-97.

Reid, A. J., Farrell, M. J., Luke, M. N., & Chapman, L. J. (2013). Implications of hypoxia tolerance for wetland refugia use in Lake Nabugabo, Uganda. *Ecology of Freshwater Fish*, *22*(3), 421-429.

Resh, V. H., Brown, A. V., Covich, A. P., Gurtz, M. E., Li, H. W., Minshall, G. W., ... & Wissmar, R. C. (1988). The role of disturbance in stream ecology. *Journal of the North American benthological society*, *7*(4), 433-455.

Lane, S. N., & Richards, K. S. (1997). Linking river channel form and process: time, space and causality revisited. *Earth Surface Processes and Landforms: The Journal of the British Geomorphological Group*, *22*(3), 249-260.

Richter, B. D., Baumgartner, J. V., Powell, J., & Braun, D. P. (1996). A method for assessing hydrologic alteration within ecosystems. *Conservation biology*, *10*(4), 1163-1174.

Roghair, C. N., Dolloff, C. A., & Underwood, M. K. (2002). Response of a brook trout population and instream habitat to a catastrophic flood and debris flow. *Transactions of the American Fisheries Society*, *131*(4), 718-730.

Rolls, R. J., Heino, J., & Chessman, B. C. (2016). Unravelling the joint effects of flow regime, climatic variability and dispersal mode on beta diversity of riverine communities. *Freshwater biology*, *61*(8), 1350-1364.

Ruhí, A., Holmes, E. E., Rinne, J. N., & Sabo, J. L. (2015). Anomalous droughts, not invasion, decrease persistence of native fishes in a desert river. *Global change biology*, *21*(4), 1482-1496.

Schnauder, I., Rudnick, S., Garcia, X. F., & Aberle, J. (2010). Incipient motion and drift of benthic invertebrates in boundary shear layers. In *River Flow 2010: Proceedings of the Fifth International Conference on Fluvial Hydraulics, Braunschweig, Germany. BAW, Karlsruhe, Germany* (pp. 1453-1461).

Schomaker, C., & Wolter, C. (2011). The contribution of long-term isolated water bodies to floodplain fish diversity. *Freshwater Biology*, *56*(8), 1469-1480.

Schwartz, J. S., & Herricks, E. E. (2005). Fish use of stage-specific fluvial habitats as refuge patches during a flood in a low-gradient Illinois stream. *Canadian Journal of Fisheries and Aquatic Sciences*, *62*(7), 1540-1552.

Stanford, J. A., & Ward, J. V. (1983). Insect species diversity as a function of environmental variability and disturbance in stream systems. In *Stream Ecology* (pp. 265-278). Springer, Boston, MA.

Stolz, C., Grunert, J., & Fülling, A. (2013). Quantification and dating of floodplain sedimentation in a medium-sized catchment of the German uplands: a case study from the Aar Valley in the southern Rhenish Massif, Germany. *DIE ERDE–Journal of the Geographical Society of Berlin*, *144*(1), 30-50.

Sukhodolov, A., Bertoldi, W., Wolter, C., Surian, N., & Tubino, M. (2009). Implications of channel processes for juvenile fish habitats in Alpine rivers. *Aquatic Sciences*, *71*(3), 338.

Suren, A. M., Biggs, B. J., Kilroy, C., & Bergey, L. (2003). Benthic community dynamics during summer low-flows in two rivers of contrasting enrichment 1. Periphyton. *New Zealand journal of marine and freshwater research*, *37*(1), 53-70.

Stoffels, R. J., Rehwinkel, R. A., Price, A. E., & Fagan, W. F. (2016). Dynamics of fish dispersal during river-floodplain connectivity and its implications for community assembly. *Aquatic sciences*, *78*(2), 355-365.

Thompson, D. M., Wohl, E. E., & Jarrett, R. D. (1999). Velocity reversals and sediment sorting in pools and riffles controlled by channel constrictions. *Geomorphology*, *27*(3-4), 229-241.

Tockner, K., Malard, F., & Ward, J. V. (2000). An extension of the flood pulse concept. *Hydrological processes*, *14*(16-17), 2861-2883.

Torgersen, C. E., Price, D. M., Li, H. W., & McIntosh, B. A. (1999). Multiscale thermal refugia and stream habitat associations of chinook salmon in northeastern Oregon. *Ecological Applications*, *9*(1), 301-319.

Townsend, C. R. (1989). The patch dynamics concept of stream community ecology. *Journal of the North American Benthological Society*, *8*(1), 36-50.

Van de Wolfshaar, K. E., Middelkoop, H., Addink, E., Winter, H. V., & Nagelkerke, L. A. J. (2011). Linking flow regime, floodplain lake connectivity and fish catch in a large river-floodplain system, the Volga–Akhtuba floodplain (Russian Federation). *Ecosystems*, *14*(6), 920-934.

Van Looy, K., Tonkin, J. D., Floury, M., Leigh, C., Soininen, J., Larsen, S., ... & Datry, T. (2019). The three Rs of river ecosystem resilience: Resources, recruitment, and refugia. *River Research and Applications*, *35*(2), 107-120.

van Vliet, M. T., Franssen, W. H., Yearsley, J. R., Ludwig, F., Haddeland, I., Lettenmaier, D. P., & Kabat, P. (2013). Global river discharge and water temperature under climate change. *Global Environmental Change*, *23*(2), 450-464.

Vezza, P., Parasiewicz, P., Spairani, M., & Comoglio, C. (2014). Habitat modeling in high-gradient streams: the mesoscale approach and application. *Ecological Applications*, *24*(4), 844-861.

Webb, A., Chee, Y. E., King, E., Stewardson, M., Zorriasateyn, N., & Richards, R. (2010). Evidence-based practice for environmental water planning in the Murray-Darling Basin.

Welcomme, R. L. (1979). *Fisheries ecology of floodplain rivers [tropics]*. Longman.

Weng, Z., Mookerji, N., & Mazumder, A. (2001). Nutrient-dependent recovery of Atlantic salmon streams from a catastrophic flood. *Canadian Journal of Fisheries and Aquatic Sciences*, *58*(8), 1672-1682.

Wetter, O., Pfister, C., Weingartner, R., Luterbacher, J., Reist, T., & Trösch, J. (2011). The largest floods in the High Rhine basin since 1268 assessed from documentary and instrumental evidence. *Hydrological Sciences Journal*, *56*(5), 733-758.

White, R. S., McHugh, P. A., & McIntosh, A. R. (2016). Drought survival is a threshold function of habitat size and population density in a fish metapopulation. *Global change biology*, *22*(10), 3341-3348.

Winemiller, K. O., Montaña, C. G., Roelke, D. L., Cotner, J. B., Montoya, J. V., Sanchez, L., ... & Layman, C. A. (2014). Pulsing hydrology determines top-down control of basal resources in a tropical river–floodplain ecosystem. *Ecological Monographs*, *84*(4), 621-635.

Wolman, M. G., & Miller, J. P. (1960). Magnitude and frequency of forces in geomorphic processes. *The Journal of Geology*, *68*(1), 54-74.

Wolter, C., & Arlinghaus, R. (2003). Navigation impacts on freshwater fish assemblages: the ecological relevance of swimming performance. *Reviews in Fish Biology and Fisheries*, *13*(1), 63-89.

Wolter, C., Buijse, A. D., & Parasiewicz, P. (2016). Temporal and spatial patterns of fish response to hydromorphological processes. *River Research and Applications*, *32*(2), 190-201.

Wood, P. J., Agnew, M. D., & Petts, G. E. (2000). Flow variations and macroinvertebrate community responses in a small groundwater-dominated stream in south-east England. *Hydrological Processes*, *14*(16-17), 3133-3147.

Zieliński, P., Gorniak, A., & Piekarski, M. K. (2009). The effect of hydrological drought on chemical quality of water and dissolved organic carbon concentrations in lowland rivers. *Pol. J. Ecol*, *57*(2), 217-227.

Dhungel, S., Tarboton, D.G., Jin, J. and Hawkins, C.P. (2016) Potential Effects of Climate Change on Ecologically Relevant Streamflow Regimes. River Research and Applications 32(9), 1827-1840.

Döll, P. and Zhang, J. (2010) Impact of climate change on freshwater ecosystems: a global-scale analysis of ecologically relevant river flow alterations. Hydrology and Earth System Sciences 14(5), 783-799.

Guse, B., Kail, J., Radinger, J., Schröder, M., Kiesel, J., Hering, D., Wolter, C. and Fohrer, N. (2015) Eco-hydrologic model cascades: Simulating land use and climate change impacts on hydrology, hydraulics and habitats for fish and macroinvertebrates. Science of the Total Environment 533, 542-556.

Jaeger, K.L., Olden, J.D. and Pelland, N.A. (2014) Climate change poised to threaten hydrologic connectivity and endemic fishes in dryland streams. Proceedings of the National Academy of Sciences 111(38), 13894.

Kakouei, K., Kiesel, J., Domisch, S., Irving, K.S., Jähnig, S.C. and Kail, J. (2018) Projected effects of Climate-change-induced flow alterations on stream macroinvertebrate abundances. Ecology and Evolution 8(6), 3393-3409.

Kuemmerlen, M., Schmalz, B., Cai, Q., Haase, P., Fohrer, N. and Jähnig, S.C. (2015) An attack on two fronts: predicting how changes in land use and climate affect the distribution of stream macroinvertebrates. Freshwater Biology 60(7), 1443-1458.

Laizé, C.L.R., Acreman, M.C., Schneider, C., Dunbar, M.J., Houghton-Carr, H.A., Flörke, M. and Hannah, D.M. (2013) PROJECTED FLOW ALTERATION AND ECOLOGICAL RISK FOR PAN-EUROPEAN RIVERS. River Research and Applications 30(3), 299-314.

Morales-Marin, L., Rokaya, P., Sanyal, P.R., Sereda, J. and Lindenschmidt, K.-E. (2019) Changes in streamflow and water temperature affect fish habitat in the Athabasca River basin in the context of climate change. Ecological Modelling 407, 108718.

Morid, R., Delavar, M., Eagderi, S. and Kumar, L. (2016) Assessment of climate change impacts on river hydrology and habitat suitability of Oxynoemacheilus bergianus. Case study: Kordan River, Iran. Hydrobiologia 771(1), 83-100.

Muñoz-Mas, R., Lopez-Nicolas, A., Martinez-Capel, F. and Pulido-Velazquez, M. (2016) Shifts in the suitable habitat available for brown trout (Salmo trutta L.) under short-term climate change scenarios. Science of the Total Environment 544, 686-700.

Mustonen, K.-R., Mykrä, H., Marttila, H., Sarremejane, R., Veijalainen, N., Sippel, K., Muotka, T. and Hawkins, C.P. (2018) Thermal and hydrologic responses to climate change predict marked alterations in boreal stream invertebrate assemblages. Global Change Biology 24(6), 2434-2446.

O'Keeffe, J., Piniewski, M., Szcześniak, M., Oglęcki, P., Parasiewicz, P. and Okruszko, T. (2018) Index-based analysis of climate change impact on streamflow conditions important for Northern Pike, Chub and Atlantic salmon. Fisheries Management and Ecology 0(0).

Papadaki, C., Soulis, K., Muñoz-Mas, R., Martinez-Capel, F., Zogaris, S., Ntoanidis, L. and Dimitriou, E. (2016) Potential impacts of climate change on flow regime and fish habitat in mountain rivers of the south-western Balkans. Science of the Total Environment 540, 418-428.

Piniewski, M., Laize, C.L.R., Acreman, M.C., Okruszko, T. and Schneider, C. (2014) Effect of Climate Change on Environmental Flow Indicators in the Narew Basin, Poland. Journal of Environmental Quality 43(1), 155-167.

Stagl, C.J. and Hattermann, F.F. (2016) Impacts of Climate Change on Riverine Ecosystems: Alterations of Ecologically Relevant Flow Dynamics in the Danube River and Its Major Tributaries. Water 8(12).

van Vliet, M.T.H., Ludwig, F. and Kabat, P. (2013) Global streamflow and thermal habitats of freshwater fishes under climate change. Climatic Change 121(4), 739-754.

Viganò, G., Confortola, G., Fornaroli, R., Cabrini, R., Canobbio, S., Mezzanotte, V. and Bocchiola, D. (2015) Effects of Future Climate Change on a River Habitat in an Italian Alpine Catchment. Journal of Hydrologic Engineering 21.

Vigiak, O., Lutz, S., Mentzafou, A., Chiogna, G., Tuo, Y., Majone, B., Beck, H., de Roo, A., Malagó, A., Bouraoui, F., Kumar, R., Samaniego, L., Merz, R., Gamvroudis, C., Skoulikidis, N., Nikolaidis, N.P., Bellin, A., Acuňa, V., Mori, N., Ludwig, R. and Pistocchi, A. (2018) Uncertainty of modelled flow regime for flow-ecological assessment in Southern Europe. Science of the Total Environment 615, 1028-1047.

Woznicki, S.A., Nejadhashemi, A.P., Tang, Y. and Wang, L. (2016) Large-scale climate change vulnerability assessment of stream health. Ecological Indicators 69, 578-594.